# THE IMPORTANCE OF FINE-SCALE FLOW PROCESSES AND FOOD AVAILABILITY IN THE MAINTENANCE OF SOFT-SEDIMENT COMMUNITIES

by

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## Abstract

Although the association between soft-sediment invertebrates and a specific sediment type has been documented for many habitats, most studies have been correlative and have failed to convincingly demonstrate any single mechanism to explain this association. Sediment type has generally been characterized by grain size, however, many other potential causal factors correlate with grain size, including organic content, microbial content, stability, food supply, and larval supply. One hypothesis for animal-sediment associations is that settling larvae are transported as passive particles and are sorted into different sedimentary habitats much like sediment grains.

To test the hypothesis that near-bed hydrodynamics may modify larval settlement, field and flume experiments were conducted where larval settlement was compared between microdepositional environments (small depressions) and non-trapping environments (flush treatments). Depressions have been observed to trap passive particles, and these experiments were therefore designed to test whether settling larvae would be trapped in depressions like passive particles. Flume flow simulations were carried out with the polychaete *Capitella* sp. I and the bivalve *Mulinia lateralis*. Experiments with flush and depression sediment treatments were conducted in the absence of the potentially confounding effects of suspended sediment and organic matter and therefore offered a highly controlled, explicit test of passive hydrodynamic deposition of larvae in depressions. Although larvae of both species were generally able to actively select a high-organic sediment over a low-organic alternative with a comparable grain size, elevated densities of both species were observed in depressions for a given sediment treatment. Thus, both species appeared to be vulnerable to hydrodynamic trapping. *M. lateralis* larvae, however, often made a "poor choice" by settling in high numbers in depressions containing the low-organic sediment while *Capitella* sp. I larvae were generally able to "escape" from depressions if the sediment was unsuitable. In field experiments carried out at Station R in Buzzards Bay, Massachusetts, significantly higher densities of *Mediomastus ambiseta* juveniles, spionid polychaete juveniles, bivalves, gastropod larvae, and nemerteans were observed in depressions compared with flush treatments over 5 relatively short experimental periods (3 or 4 days each) during the summer of 1990. Of the abundant taxa, only *Capitella* spp. was not significantly more abundant in depressions compared with flush treatments, although numbers tended to be higher in depressions. Experiments were conducted over a short time period to minimize potential biological interactions between taxa and reduce the likelihood that organic material would accumulate in depressions and provide a cue for settling larvae. Thus, higher numbers in depressions suggest that larvae were passively entrained. These flume and field experiments suggest that near-bed hydrodynamics may modify settlement at some scales, and that both active and passive processes may operate in determining larval distributions in shallow-water, muddy habitats.

In deep-sea ecosystems, the role of near-bed hydrodynamics is also of interest because of the potential role that larval settlement in organic patches may play in maintaining the immense species diversity characteristic of many deep-sea ecosystems. To try to understand the role of organic patches in deep-sea communities, several investigators have used colonization trays containing sediments that have been treated in different ways. These experiments have been criticized in the past because the sediment surface in the trays was elevated above the bottom and may therefore have interfered with natural

boundary layer flow. Flume simulations of flow over these colonization trays revealed serious flow artifacts generated by the trays, and that flow across the sediment surface of the trays was characterized by turbulent eddies, accelerated velocities and boundary layer thickening. These sorts of flow characteristics would not be expected over natural sediments, and an alternative colonization tray was designed to eliminate these artifacts.

To test the hypothesis that different types of food patches would result in different types of larval response, and determine how near-bed hydrodynamics may influence larval settlement, flush colonization trays filled with prefrozen sediment were deployed in tandem with artificial depressions south of St. Croix, U.S.V.I at 900 m depth. Colonization trays and artificial depressions were either unenriched or enriched with *Thalassiosira* sp. and *Sargassum* sp. two types of algae chosen to mimic natural food patches on the sea floor. Unexpectedly high densities of organisms colonized trays after only 23 days. The *Thalassiosira* trays were colonized by high densities of a relatively low diversity, opportunistic fauna, *Sargassum* trays were colonized by lower densities of a higher diversity fauna, and unenriched trays were colonized by very low numbers of a very diverse fauna. All tray faunas were markedly different in composition from the natural, ambient fauna. These findings suggest that different patch types did, indeed, result in a specialized faunal response to each of the "patch" types. Depressions on the sea floor provide a natural mechanism for food patch formation because passive particles such as detritus and algae tend to be entrained in the depressions. To determine whether dominant colonizers would be entrained in depressions like passive particles or could differentiate between depression "patch" types in a flow environment that might be expected to make active selection more difficult, artificial depressions were unenriched or enriched with *Sargassum* sp. or *Thalassiosira* sp. Total densities of organisms and densities of the most abundant species were substantially lower in artificial depressions than in trays. Densities in *Thalassiosira* depressions were lower than in *Sargassum* depressions and densities in unenriched depressions were extremely low, suggesting that dominant colonizers were not passively entrained in depressions and that colonization was specialized and highly active for these taxa. A different fauna was also observed in natural depressions compared with flush sediments, suggesting that natural depressions do contribute to species coexistence. Long-term tray deployments designed to test whether different faunas would be present in "patches" of different ages indicated that time may also play an important part in a deep-sea patch mosaic.

Thesis Supervisor: Dr. Cheryl Ann Butman, Associate Scientist, Woods Hole Oceanographic Inst.

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## INTRODUCTION

Since Peterson's (1913) description of Danish soft-sediment benthic communities, numerous investigators have documented distributions of communities in relation to physical factors, leading to the generalization that many species are associated with sediments of a particular grain size (e.g., Gray, 1974; Rhoads, 1974). A number of mechanisms have been proposed to explain this association, including active response by organisms to grain size, organic content or microorganisms, amensalistic interactions, larval supply, and food supply. An extensive review of the existing information on animal-sediment relationships (see Chapter 1) indicated that strong experimental evidence to support any of these hypotheses is lacking, largely because most studies on animal-sediment associations are correlative, and thus have failed to differentiate between interrelated mechanisms. Indeed, the relationship between sediment type and bottom flow is very complicated in itself, and how this relates to the distributions of marine organisms is unlikely to emerge without extensive, controlled experimentation that is sorely lacking at present.

One hypothesis to explain the association of organisms with a particular sediment type is that planktonic larvae of benthic species behave as passive particles and are sorted by near-bottom flow into different sedimentary habitats much like sediment grains (e.g., Butman, 1987). This could result in sediment-specific distributions where no causal relationship between grain size and faunal distribution exists. There is good reason to suspect that near-bottom flows may influence larval distribution and settlement

locale. Many larvae may encounter velocities that exceed their maximum swim speeds at heights corresponding to only a few bodylengths above the bottom (Butman, 1986). Testing the relative importance of near-bed flow on larval distribution is problematic because it is difficult to experimentally manipulate flow on a large scale *in situ*, and many other factors are also related to bottom flow. To circumvent this problem, several investigators have manipulated flow on a very small scale to determine what effect that manipulation would have on larval settlement. Using this approach, Eckman (1979, 1983) and Savidge and Taghon (1988) showed that in high-energy, sandflat communities, fine-scale flow processes did affect larval settlement patterns. Sediment trap studies in a muddy habitat suggest that larvae are collected in traps with different collection efficiencies as would be predicted for passive particles (Butman, 1989). This sort of fine-scale manipulation was utilized in the work described in this thesis.

Small depressions on the sea floor create a region of reduced velocity shear where passive particles tend to accumulate (e.g. Nowell and Jumars, 1984). Thus, it is possible to create localized areas with very different flow characteristics to determine how larval settlement and distributions are affected. In intertidal and shallow, subtidal sandflats, elevated densities of organisms have been noted in natural (e.g., VanBlaricom, 1982) and artificial (e.g., Savidge and Taghon, 1988) depressions compared with flush sediments. Although higher densities may have resulted from active response by settling larvae to elevated organic matter (e.g., VanBlaricom, 1982), an alternative explanation is that larvae were passively entrained within the depression (e.g., Savidge and Taghon, 1988). To test this idea in a relatively low-energy, muddy habitat, colonization trays

originally designed to minimize flow disturbance were placed on the ocean bottom. Some trays were flush with the ocean bottom and others were placed to form a small depression that would accumulate passive particles; both trays contained similar sediment treatments that were expected to be favorable to settling larvae. Thus, if larval distribution is heavily influenced by near-bottom flow, then higher densities of larvae would be expected to settle in depression trays compared with flush trays. Although experiments were run for a short period of time (3 or 4 days) to reduce the potentially confounding effects of organic matter accumulation and between-species interactions, the experimental design could not completely eliminate these effects. Therefore, complementary flume flow experiments with small depressions were conducted using larvae of *Capitella* sp. I and *Mulinia lateralis*, where the potentially confounding effects of suspended sediment and organic matter were eliminated. Flume simulations were conducted with only one species at a given time, precluding potential species interactions that could complicate data interpretation. In the flume experiments, several sediment types could be tested in a given experiment, and although it has previously been shown that these species are capable of habitat selection (e.g., Butman *et al.*, 1988; Grassle *et al.*, 1992a, b; Butman and Grassle, 1992), it is unclear exactly how larvae select. The goal of these experiments was to determine whether settlement by larvae capable of habitat selection could be modified by bottom flow such that larvae would make "mistakes" and accumulate in depressions containing an unfavorable sediment type. If indeed, "mistakes" were made, it would indicate that fine-scale processes do influence larval settlement, and that larvae may be dependent on bottom flow to bring

them into contact with a suitable sediment. In these experiments, sediment choices were similar in grain size but very different in organic content, and given that both of the species tested tend to be associated with organic-rich sediments, the "poor choice" was the organic-poor sediment.

In the deep sea, patchy distributions in relation to food are likely more important than animal-sediment associations given that rapid changes in sediment composition are less likely to be observed over small spatial scales than in shallow-water communities (e.g., Maciolek *et al.*, 1986). Deep-sea communities have recently been shown to be extremely species rich, perhaps rivalling tropical rain forests in terms of numbers of species present (Grassle and Maciolek, 1992). One explanation for such high diversity in an apparently homogeneous habitat is that small scale patches of food create microhabitats on which colonizing fauna may specialize (Grassle and Sanders, 1973), thus allowing large numbers of species to coexist. In the past, several investigators have used treated sediments in colonization trays to determine how quickly organisms settle in unoccupied sediment, both in shallow water (e.g. McCall, 1977) and in the deep sea (e.g. Grassle, 1977; Desbruyères *et al.*, 1980, Grassle and Morse-Porteous, 1987). Many of these studies have been criticized, however, because colonization trays may have created considerable flow disturbance (Smith, 1985). Given the present interest in small-scale hydrodynamic effects on larval settlement discussed above, one goal of the present study was to describe these flow artifacts and design an alternative type of colonization tray that would allow smooth, natural flow over the tray's sediment surface.

Trays designed to eliminate potential flow artifacts were used to test whether different organisms would respond to different patch types, where different food "patches" were created in trays deployed in a deep-sea habitat south of St. Croix, U.S.V.I. Some trays were unenriched and others were enriched with *Thalassiosira* sp. or *Sargassum* sp., two types of algae chosen to mimic natural food patches on the deep sea floor. The goal of the experiment was to determine whether different fauna would respond to each of the algal treatments and how this fauna would compare with unenriched trays and the fauna in the ambient sediment. This would clarify whether specialized faunas were attracted to each of the patch types. In addition, artificial depressions were created; some were not enriched and others were enriched with *Thalassiosira* sp. or *Sargassum* sp. As with the shallow water experiments, the goal was to determine whether larvae would accumulate in depressions like passive particles, and whether they would be able to differentiate between patch types when near-bed flow conditions were altered in a way that would tend to trap passive colonizers.

Thus, the overall goal of this work was to determine experimentally how settling larvae in shallow-water and deep-sea habitats are able to choose where they settle, to what degree selection is dependent on sedimentary organic content, and how near-bed hydrodynamics may influence the distribution of settling larvae. Until these sorts of questions are approached using carefully designed, experimental techniques, the relative importance of the many factors contributing to the distributional ecology of benthic organisms is likely to remain poorly understood.

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# Chapter 1

## Animal-Sediment Relationships Revisited:

## What Do We Really Know About Cause and Effect?

This chapter has been written jointly with Cheryl Ann Butman for submission to Oceanography and Marine Biology: An Annual Review. The format reflects that of the journal.

**ABSTRACT** Over the last few decades, many studies have correlated infaunal invertebrate distributions with sediment grain size, leading to the generalization of distinct associations between animals and sediments. The most touted associations were deposit feeders with muddy sediments and suspension feeders with sandy sediments. Proposed causative factors have included grain size per se, organic content, microbial content, trophic- and species-specific interactions and food supply. An early predominant hypothesis to explain the association of suspension feeders with sandy sediments was that they are excluded from muddy habitats by amensalistic interactions with deposit feeders. There is, in fact, little evidence for the pattern that this hypothesis purports to explain and the proposed underlying mechanism oversimplifies sediment-transport dynamics. Furthermore, animal-sediment relationships have been evaluated primarily using sediment and biological samples that have been integrated over vertical scales within the bed that are larger than those relevant to most organisms. Moreover, sediment grain size was usually determined on completely disaggregated samples and these grain-size distributions may not be biologically or hydrodynamically meaningful.

Critical re-examination of data on animal-sediment relationships suggests that many species are not always associated with a single sediment type, and that suspension and deposit feeders often co-occur in large numbers. Furthermore, because of recent demonstrations of feeding plasticity in a number of infaunal species, the simple dichotomy of suspension versus deposit feeding is no longer valid. Likewise, in most studies that have tested or evaluated trophic-group amensalism, the hypothesis generally was qualified to such a degree that it is no longer meaningful. We suggest that the

complexity of soft-sediment communities may defy any simple paradigm and propose a new focus on the gestalt of the sediment milieu, which includes both static sediment and dynamic flow factors. We propose that some of the factors such as sediment grain size, flow regime, and sediment-transport rate may shape distributions of species in soft-sediment environments; however, these variables are so strongly correlated with each other that it may not be meaningful to separate their effects since they co-vary in nature. As specific examples of the complex relationships between organism distributions and environmental and biological parameters, we summarise existing information on the distribution and ecology of two infaunal species that are better studied than most, the bivalve Mercenaria mercenaria and the polychaete Owenia fusiformis. Distributional and experimental data on these two species do not consistently support the amensalism hypothesis. These data also illustrate the complexity of animal-sediment relationships and the modest level of our present understanding of, especially, the role of the near-bed flow and sedimentary environment in determining infaunal distributions.

Most studies of animal-sediment associations were conducted at a time when the complex, dynamic relationship between bottom sediments and near-bed hydrodynamics were poorly understood, and the recently expanding interest in coastal sediment transport and its controlling mechanisms has created an entirely new framework for studying organism-sediment interactions. We re-evaluate animal-sediment relationships in this light, reviewing what is known about factors that should be added to the list of those likely to limit or delimit distributions of infaunal organisms -- physical factors (hydrodynamic regime and sediment-transport regime) that directly correlate with and

are the causative processes responsible for sediment distributions, and factors (food supply and larval supply) that indirectly correlate with sediment distributions. A multidisciplinary study of the biology, geology, hydrodynamics and sediment transport on Georges Bank, U.S.A., is used to illustrate the complexity and dynamic nature of near-shore, sedimentary environments and animal-sediment relationships therein. In conclusion we recommend research directions that may help clarify cause and effect, emphasizing manipulative experiments and sampling that may be more biologically and physically meaningful as compared to previous correlative studies.

# INTRODUCTION

The relationship between the distribution of infaunal invertebrate species and the sediments in which they reside has been the subject of numerous correlative studies, some experimental manipulations, and several syntheses and reviews during the three or so decades since Thorson (1957) developed the concept of "parallel level-bottom communities". Unfortunately, a universally predictive and cogent explanation for observed "animal-sediment relationships" has yet to stand firmly the test of time. This may reflect fundamental deficiencies in the conceptualization of the issues and relevant scales, limitations in the quality and/or quantity of the data, including the paucity of experimental studies, or simply the inherent complexity of a system that may defy a simple paradigm. This review addresses these alternatives in the spirit of the opening statements of Hutchinson's (1953) address to the Academy of Natural Sciences of Philadelphia on "The Concept of Pattern in Ecology":

> "In any general discussion of structure, relating to an isolated part of the universe, we are faced with an initial difficulty in having no a priori criteria as to the amount of structure it is reasonable to expect. We do not, therefore, always know, until we have had a great deal of empirical experience, whether a given example of structure is very extraordinary, or a mere trivial expression of something which we may learn to expect all the time."

Indeed, the significance of animal-sediment associations is difficult to evaluate because

the mechanism(s) determining the distributions of organisms is so poorly understood. The growing appreciation for the influence of hydrodynamics and sediment transport on benthic biological processes (e.g., Nowell & Jumars, 1984; C.A. Butman, 1987; Palmer, 1988a; Miller & Sternberg, 1988), and the contemporary view of bottom boundary-layer flow and sediment-transport processes in general (e.g., Nowell, 1983; B. Butman, 1987a, b; Grant & Madsen, 1986; Cacchione & Drake, 1990) warrants a re-examination of the information on animal-sediment relationships.

This review evaluates whether the data exist to support the generalisation of distinct animal-sediment relationships and critically examines the experimental evidence for the mechanism(s) that may produce such associations. In contrast to previous reviews (e.g., Purdy, 1964; Gray, 1974, 1981; Rhoads, 1974; Pèrés, 1982; Probert, 1984), we are impressed with the lack of convincing evidence that animal distributions are determined by any of the classical parameters of grain size, organic content, micro-organisms and sediment "stability". These findings are discussed relative to a contemporary conceptualisation of the dynamic nature of the soft-sediment milieu and potential adaptations of the infauna to this environment. Like others (e.g., Jumars & Nowell, 1984b), we suggest that more meaningful and predictive explanations for infaunal distributions may emerge if, in addition to experimental evaluation of traditional sediment and biological factors, distributions are evaluated relative to the hydrodynamic and sediment-transport processes that are responsible for sediment distributions. We propose a new focus on the gestalt of the sedimentary milieu (taken here to include biological, chemical, and physical factors), rather than individual, isolated factors which

have been difficult (sometimes impossible) to test independently and, because of their interdependence, such single-factor experiments have largely yielded ambiguous results. We must take advantage of the recent extraordinary developments in our conceptual understanding of the processes responsible for surficial sediment distributions, the innovative instrumentation now available to measure many important aspects of the benthic boundary layer environment, including biological, chemical, and physical characteristics, and the mounting enthusiasm for interdisciplinary research in oceanography to conduct experiments that embrace the dynamic nature of soft sediments in the ocean.

In this review we define "infauna" to include those benthic invertebrates that live largely within the sediment bed, including animals traditionally referred to as "macrofauna" (i.e., those animals retained on 500 or 300 μm sieves) and "meiofauna" (i.e., those animals that are smaller than macrofauna but are retained on a 63 μm sieve), though our own interests in macrofaunal biology are certainly reflected in the studies we have chosen to include. We also acknowledge that this review is not exhaustive, but omissions of references reflect only our naivete and no conscious decision of exclusion. Because we are much more familiar with the North American literature and, because of logistics, we have reviewed little of the literature on this subject that is written in languages other than English. We hope the review is not badly biased by our North American perspective.

In this paper we do not specifically review the potential role of biological interactions (e.g., competition and predation) in determining infaunal distributions, but

there is no doubt that distributions of many soft-sediment invertebrates are influenced (sometimes greatly) by other species. The emphasis here is placed largely on abiotic factors because species interactions do not necessarily explain how animal-sediment associations are initially established. For example, a species may only occur in sandy sediments because another species out-competes it elsewhere, but this does not explain why the dominant competitor does not occur in sands. Thus, at some level, animal-sediment relationships are likely to be important. Furthermore, abiotic factors such as fluid flow and sediment-transport processes can also determine how and if an organism colonizes a given habitat, and initial colonization obviously precedes subsequent interactions among recruits. Nonetheless, we have no intention of down-playing the potential importance of biological interactions in infaunal community structure, but because this topic was recently reviewed by Wilson (1991), it would be redundant to do so again here.

## EVIDENCE FOR DISTINCT ASSOCIATIONS BETWEEN INFAUNA AND SEDIMENTS

### HISTORICAL PERSPECTIVE

The formal study of animal-sediment associations began with the classification of bottom communities based on dominant species by Petersen (1913), who noted, among other factors, that communities differed among bottom types. Greater importance was placed on bottom type by Ford (1923), who suggested that substrate was a key factor

contributing to community differences, and Davis (1925), who suggested that grain-size groupings could be used to predict dominant taxa. Synthesizing existing data on communities from the North Sea, Jones (1950) placed "communities" and "zones" into specific sediment types, noting that differences in the supply of detritus and organism mobility might contribute to observed patterns. Still, when Thorson (1957) synthesized the available data on infaunal distributions, developing the concept of "parallel level-bottom communities", very few studies actually included quantitative information on the sediments (e.g., grain-size distributions) in which the organisms were collected (some exceptions include, for example, Ford, 1923; Spärck, 1933; Stephen, 1933; Thorson & Ussing, 1934; Holme, 1949). In fact, it was the dual effect of Thorson's (1957) generalisations and Sanders' (1958) observation that different infaunal feeding types tended to dominate sandy versus muddy sediments that prompted the plethora of subsequent studies of the relationship between distributions of infauna and sediments (e.g., Table I). Although a variety of collection and processing techniques were used, the premise and goals of these studies were similar -- to describe patterns of distribution and, in most instances, at least suggest an underlying mechanism to account for such distributions.

The mechanism proposed by Sanders (1958) to account for observed associations between infauna and sediments was that differences in food supply resulted in the domination of sandy habitats by suspension feeders and muddy habitats by deposit feeders. The data forming the basis for Sanders' (1958) and most subsequent hypotheses concerning animal-sediment relationships consist of comparisons between

Table I. Benthic studies on animal-sediment associations in marine habitats. Studies that did not specifically compare animal distributions to bottom type in some way are not included. "Not given" does not suggest analysis was not performed; it indicates that methodology was not described. Studies were chosen to be representative and the table is not exhaustive in coverage. Question marks in the table denote instances where information was vague and some inference was necessary.

| STUDY | AREA | SEDIMENT TYPES | SPECIES | ASSOCIATION/ ANALYSIS[1] | COMMENTS | SAMPLING GEAR | VERTICAL INTEGRATION | GRAIN SIZE/ CARBON |
|---|---|---|---|---|---|---|---|---|
| Petersen (1913) | Danish coast | Sand to mud | Community | Yes/ Correlative | Strong groupings described as statistical, not biological units | Petersen grab, trawls | 3 cm or greater | Visual/ Kjeldahl (1891) |
| Ford (1923) | Plymouth, U.K. | Sand to mud | Community | Yes/ Correlative | Petersen type groupings though some species not sediment specific | Petersen grab? | 3 cm or greater? | Not given/ Not done |
| Spärck (1933) | East Greenland | Sand to mud | Community | Yes/ Correlative | Extended Petersen's communities but no discussion of mechanism | Petersen grab | entire grab | Visual/ Not done |
| Stephen (1933) | North Sea, U.K. | Sand to mud | Molluscs | Yes/ Correlative | Extreme sediment groupings gave good separation of communities | Petersen grab & shovel | 15 cm | Visual/ Not done |
| Thorson & Ussing (1934) | East Greenland | Sand to mud | Community | Yes/ Correlative | Groupings similar to 1913 study though some discrepencies | Petersen grab | 3 cm or greater | Visual/ Not done |
| MacGinitie (1935) | Elkhorn Slough, California | Sand to mud | Community | No/ Correlative | Several common species widespread over habitats | Shovel | 2-3 feet? | Visual/ Not done |
| Holme (1949) | Exe Estuary, U.K. | Sand to mud | Community | Yes/ Correlative | Distributions related to silt content, organic carbon mentioned | Shovel? | 6 inches | Piper (1942)/ Not done |
| Smidt (1951) | Danish Wadden Sea | Sand to mud | Community | Yes/ Correlative | General association of most species with one bottom type | Tube core | 3 cm | Visual/ Not done |
| Pratt (1953) | Narragansett Bay, Rhode Island | Sand to mud | Mercenaria | Yes/ Transplants | Most common in shell/rock Faster growth in sand | Dredge | Not given | Visual/ Not done |
| Sanders (1956) | Long Island Sound, New York | Sand to mud | Community | Yes/ Correlative | No replication within site and date | Forster anchor dredge | 7.6 cm | Bouyoucous (1936)/ Not done |
| Sanders (1958) | Buzzards Bay, Massachusetts | Sand to mud | Community | Yes/ Correlative | No within site replication. | Forster anchor dredge | 7.6 cm | Wet sieve & pipette*/ Not done |

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|---|---|---|---|---|---|---|---|---|
| Longhurst (1958) | West Africa | Sand to mud | Community | No/ Correlative | Only a few species sediment specific | Dredges, grabs | unknown | Dry dispersed sieve/ Not done |
| Webb & Hill (1958) | Laos Lagoon, | Sand to mud | Branchiostoma nigeriense | Yes/ Correlative & experimental | Trial and error sediment selection in lab supported field pattern of sand preference | Not given | Not given | Wet sieve/ calcined silt |
| Wieser (1959) | Puget Sound, Washington | Coarse to fine sand | Community | Yes/ Correlative | Suggest 200μ grain size a critical distribution barrier | Small beaker | Not given | Dry sieve/ Not done |
| McNulty et al. (1962) | Biscayne Bay, U.S.A. | Sand to mud | Community | Yes/ Correlative | Filter feeders found in different grain sizes than Sanders' | Van Veen grabs | Entire grab? | Wet sieve & pipette[2]/ Not done |
| Sanders et al. (1962) | Barnstable, Massachusetts | Sand to mud | Community | No?/ Correlative | Median grain size poor predictor of community composition | Various size cores | 3, 8 or 30 cm | Wet sieve & pipette[2]/ Combustion |
| Buchanon (1963) | Northumberland Sea, U.K. | Gravel to fine sand | Community | No/ Correlative | Only a few species showed association | Van Veen grab | Entire grab? | Wet sieve & pipette[2]/ Not done |
| Wigley & McIntyre (1964) | Martha's Vineyard, Massachusetts | Sand to mud | Macrofauna & meiofauna | Yes & No/ Correlative | Total densities of macro and meiofauna related to substrate, | Smith & McIntyre grab | 4 cm or entire grab | Not given/ Not done |
| Cassie & Michael (1968) | Auckland, New Zealand | Sand to mud? | Community | Yes/ Correlative | Data presentation obtuse. Some species not sediment specific | Unknown | 5-10 cm | Wet sieve[2]/ Morgans (1956) |
| Gray (1968) | San Juan Island, Washington | Grades of sand | Leptastacus constrictus | No/ Correlative & Experimental | Field populations unrelated to organic content or bacteria but selection related to bacteria | Not given | Not given | Not done/ 2 h incineration |
| Lie (1968) | Puget Sound, Washington | Gravelly sand to mud | Community | Yes/ Correlative | Suggests contiguous communities as function of sediment gradient | Van Veen grab | entire grab | Krumbein & Pettijohn (1938)[2]/Not done |
| Gibbs (1969) | Plymouth, U.K. | Sand to mud | Polychaetes | Yes/ Correlative | General association with grain size though several species widely | Perspex corer | 12 cm | Morgans (1956)/ Not Done |

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|---|---|---|---|---|---|---|---|---|
| Lie & Kisker (1970) | Strait of Juan de Fuca, Washington, U.S.A. | Gravel to mud | Community | Yes/ Correlative | Very extreme sediment groupings gave good separation | Van Veen grab | Entire grab | Krumbein & Pettijohn (1938)[2]/Not done |
| Longbottom (1970) | Kent Coast, U.K. | Sand to fine mud | Arenicola marina | Yes/ Correlative | Association with grain size and organic content. | "surface sediment samples" | Not given | Disagg. dry sieve[2]/ Morgans (1956) |
| Nichols (1970) | Puget Sound, Washington | Fine to silty sand | Polychaetes | Yes/ Correlative | Clay content key variable and thus organic content | Van Veen grab | Entire grab | Dry sieve & pipette[2]/ Not done |
| Pearson (1970, 1971) | Scotland sea-lochs | Mud to gravel | Community | Yes & No/ Correlative | Suggests fjord enclosure results in saturation of bottom with larvae, blurring association | Van Veen grab | Entire grab | Dry sieve & pipette[2]/ Wet combustion |
| Rhoads & Young (1970) | Buzzards Bay, Massachusetts | Mud to sand | Mercenaria Nucula | Yes/ Transplant | Trophic group amensalism related to sediment type | Smith & McIntyre grab | Entire grab? | Dry sieve analyser/ Leco carbon analyser |
| Stephenson et al. (1970) | Moreton Bay, Australia | Mud to sand | Community | Yes & No/ Correlative | Weakly defined site groups conform to topography | Prawn trawls | Not given | Visual/ Not done |
| Day et al. (1971) | Beaufort, North Carolina | Sand to silty sand | Community | No/ Correlative | No relation of distribution to mean particle size | Van Veen and dredge | Entire grab | Standard Elutriation[2]/ Kjeldahl (1891) |
| Field (1971) | False Bay, South Africa | Grades of mud | Community | Yes/ Correlative | Good association with grain size and organic content | Van Veen | Entire grab | Dry sieve/ Morgans (1956) |
| Hughes & Thomas (1971) | Bideford River, Prince Edward Island, Canada | Mud to sand | Community | No/ Correlative | Only a couple of dominants sediment specific | Suction dredge | 30-50 cm | Wet sieve & pipette[2]/ Morgans (1956) |
| Johnson (1971) | Tomales Bay, California | Sand to mud | Community | Yes/ Correlative | Good association but many species "strayed" | Van Veen grab | Entire grab | Visual/ Not done |

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|---|---|---|---|---|---|---|---|---|
| Young & Rhoads (1971) | Cape Cod Bay, Massachusetts | Sand to mud | Community | No/ Correlative | Co-occurrence of deposit and suspension feeders attributed to sediment stabilization | Smith & McIntyre grab | Entire grab | Dry sieve & pipette[2]/ Leco carbon analyser |
| Bloom et al. (1972) | Old Tampa Bay, Florida | Sand to muddy sand | Community | Yes & No/ Correlative | Weak correlations as support for trophic group amensalism | 0.1 $m^2$ grab | 20-40 cm | wet sieve[2]/ combustion |
| Gage (1972) | Scottish Sea-lochs, U.K. | Sand to muddy sand | Community | Yes/ Correlative | Acknowledges grain size a key correlate of hydrodynamics | Van Veen grab | Entire grab | wet sieve & pipette[2]/ not done |
| Howard and Dorjes (1972) | Sapelo Island, Georgia | Sand and muddy sand | Community | No/ Correlative | Several species dominant in both sediment types. | 0.2 $m^2$ bulk sample | 50 cm | sediment analyser/ not done |
| Hughes et al. (1972) | St. Margarets Bay, Nova Scotia | Gravel to mud | Community | No/ Correlative | Acknowledge importance of currents, organics & other species | Van Veen | Entire grab | Krumbein & Pettijohn (1938)[2]/Not done |
| Boesch (1973) | Hampton Roads, Virginia | Sand to mud | Community | Yes/ Correlative | Pretty good assocation though different from previously cited associations. | Van Veen grab | Entire grab | Folk (1961)[2]/ Not done |
| Eagle (1973) | Liverpool Bay, U.K. | Sand and muddy sand | Community | Yes & No/ Correlative | Ratios differ but many species common in both habitats | Smith & McIntyre grab, beam trawls | Entire grab | Wet sieve & pipette[2]/ Strickland & Parsons (1968) |
| Aller & Dodge (1974) | Discovery Bay, Jamaica | Grades of sand | Community | No/ Correlative | Found absence of deposit feeders in sandy habitats | 31 cm core | 20-25 cm | Wet sieve[2]/ Not done |
| Warwick & Davies (1977) | Bristol Channel, U.K. | Sand to mud | Community | Yes/ Correlative | Admit sediment affiliation not very specific | Smith & McIntyre grab, dredge | Entire grab | Sonar & visual/ Not done |
| Mountford et al. (1977) | Chesapeake Bay, Maryland | Shell & sand to mud | Community | Yes/ Correlative | No obvious relation between trophic mode and sediment type | Forster anchor dredge | Entire grab | Buchanan & Kain (1971)/Not done |
| Tyler & Banner (1977) | Bristol Channel, U.K. | Gravelly to muddy sand | Ophiuroids | No/ Correlative | Poor correlation between adult density and sediment parameters | Shipek grab | Entire grab | Folk (1961)[2]/ Oxidation |

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|---|---|---|---|---|---|---|---|---|
| Whitlatch (1977) | Barnstable, Massachusetts | Sandy gravel to mud | Community | Yes/ Correlative | Grain size better predictor than than in Sanders et al. study | 12.5 cm core | Entire core | Wet sieve[2]/ Morgans (1956) |
| Buchanan et al. (1978) | Northumberland Coast, U.K. | Sand to silty sand | Community | Yes/ Correlative | Association with silt but long-term changes in dominants | Van Veen grab | Entire grab | Wet sieve?[2]/ Not done |
| Larsen (1979) | Sheepscot Estuary, Maine | Silty sand to Mud? | Community | No/ Correlative | No strong association but little range in sediment type | Ponar grab | Entire core | Standard method[2]/ Not given |
| Maurer et al. (1979) | Delaware Coast, U.S.A. | Gravelly sand to sandy mud | Community | Yes/ Correlative | Noted silty-sand troughs in sand environments had silty-sand fauna | Petersen grab | Entire grab | Folk (1968)/ % volatiles |
| Flint & Holland (1980) | Gulf of Mexico, Texas | Sandy mud to mud | Community | Yes & No/ Correlative | Bottom water variability more important than sediment type | Smith & McIntyre grab | Entire grab | Particle analyser/ Not done |
| Warwick & Uncles (1980) | Bristol Channel, U.K. | Sand to mud | Community | Yes/ Correlative | Relate tidal stress to distributions of organims and sediment type | Smith & McIntyre grab | Entire grab | Sonar/ Not done |
| Shin & Thompson (1982) | Hong Kong Harbour | Grades of mud | Community | Yes & No/ Correlative | Silt-clay good predictor but salinity better | Smith & McIntyre grab | Entire grab | Bouyoucos (1936)/ Combustion |
| Tourtelette & Dauer (1983) | Chesapeake Bay, U.S.A. | Sand to mud | Community | Yes & No/ Correlative | Only clean sand fauna was restricted in distribution, other fauna widespread | Ponar grab | Entire grab | |
| Shackley & Collins (1984) | Swansea Bay, U.K. | Sand to mud | Community | Yes/ Correlative | Suggests faunal associations predict gross changes in sediment | Day & Shipek grabs | Entire grab | Wet sieve[2]/ Not done |
| Coull (1985) | South Carolina, U.S.A. | Sand & mud | Meiofauna | Yes/ Correlative | Timing and magnitude of abundances varied greatly between sites | Cores | 1 to 2 cm | Folk (1968)/ Walkley & Black (1934) |
| Holland (1985) | Chesapeake Bay, U.S.A. | Sand to mud | Community | Yes/ Correlative | Many species widely distributed but different dominants | Several types of grabs | Entire grab | Not given/ Not given |

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|---|---|---|---|---|---|---|---|---|
| Rhoads et al. (1985) | East China Sea | Sand to mud | Community | Yes/ Correlative | Good associations with sediment, sedimentation also important | Spade-boxcorers & Petersen grabs | Entire grab | X-radiographs/ Not done |
| Long & Lewis (1987) | Gulf of St. Lawrence, Canada | Gravel sand to mud | Community | Yes/ Correlative | Good correlation with feeding type | Van Veen grab | Entire grab | Particle analyser/ Not done |
| Theroux & Grosslein (1987) | Georges Bank, U.S.A. | Sand to mud | Community | Yes/ Correlative | Verbally describe different faunas in mud and sand but no statitics | Smith & McIntyre grab | Entire grab | Particle analyser/ Not done |
| Weston (1988) | North Carolina, U.S.A. | Grades of sand | Community | Yes/ Correlative | Various sediment parameter related to distributions, food supply cited | Smith & McIntyre grab | Entire grab | Dry sieve/ Not done |
| Ishikawa (1989) | Oppa Bay, Japan | Sand to mud | Community | Yes/ Correlative | Good correlation with sediment grain size, organic content | Smith & McIntyre grab | Entire grab | Particle analyser/ CHN analyser |
| Junoy & Viéitez (1990) | Northwest Spain | Sand to mud | Community | Yes & No/ Correlative | Some mixing of station clusters for different sediment types | Shovel? | 30 cm | Not given/ Not given |
| Duineveld et al. (1991) | North Sea | Sand to muddy-sand | Community | Yes/ Correlative | Suggest different fauna in sediments related to local production, deposition, stress | Grabs & boxcorers | Entire grab | Not given/ Not done |
| Hyland et al. (1991) | California, U.S.A. | Sandy-mud to mud | Community | Yes/ Correlative | Oxygen & depth more important but percentage of sand also useful | Hessler-Sandia box corer | 10 cm | Not given/ Not given |
| Palaćin et al. (1991) | Western Mediterranean | Sand to mud | Community | Yes/ Correlative | Granulometry strongly related with many species' distributions | Corers | 8-20 cm | Not given/ Not given |
| Service & Feller (1992) | South Carolina, U.S.A. | Sand & mud | Community | Yes/ Correlative | Sand & mud faunas differed, with more burrowers in mud | Hand-held corers | 5-10 cm | Visual?/ Not done |

[1]Correlation denotes direct correlational analyses as well as ordination and classification techniques where sediment and biological samples were independently grouped based on similar composition and then compared. In many earlier studies no statistical comparison of any sort was made and "correlation" is used to describe an implied association based on "correlative" sampling of organisms and sediment.
[2]Although not stated as such in the original studies, we believe those studies marked with an asterisk used roughly comparable methodologies.

bulk sediment characteristics (usually the grain-size distribution integrated over the top few centimetres) and densities of dominant species, both documented over spatial scales of metres to kilometres (e.g., Table I). Of the most commonly cited studies on animal-sediment relationships (refer to Table I), most show at least some sort of relationship between faunal distribution and sediment type.

These descriptive studies have represented an important advance in our understanding of soft-sediment communities, particularly in providing an atlas of animal distributions from shallow-water habitats in many different areas of the world (Table I). As a first step towards understanding why organisms live where they do, information on the distribution of organisms is vital; however, descriptive and correlative data cannot explain why these distributions exist. They should, instead, form the foundation for guiding research directions on mechanistic relationships responsible for animal-sediment associations. What is perhaps most striking about the studies summarized in Table I is that so few provide strong evidence of causality; most studies are correlative, and sediment type is a covariant of other causative variables (e.g., Jansson's (1967b) concept of grain size as a "super parameter"). Results and conclusions of these studies must be re-evaluated within the context of our current understanding of 1) the nature of bottom sediments, sediment transport and the boundary-layer flow regime and 2) life histories and habits of benthic invertebrates under realistic field conditions, particularly with reference to larval settlement and infaunal feeding ecology.

## CONTEMPORARY VIEW

A major difficulty in interpreting most of the previously collected information on animal-sediment associations is that grain-size alone is not an adequate descriptor of the sedimentary environment, due to the complex nature of bottom sediments (e.g., Johnson, 1971, 1977; Whitlatch & Johnson, 1974; Jumars & Nowell, 1984a; Watling, 1988) and associated boundary-layer flow and sediment-transport regimes (e.g., Komar, 1976a, b; Nowell, 1983; Nowell & Jumars, 1984; Grant & Madsen, 1986). In fact, sediment grain size correlates with a number of potential causative factors (discussed later) which may explain why, in some cases, grain size may actually be a poor correlate of benthic community composition (e.g., Table I). Nephthys/Nucula communities in Buzzards Bay, Massachusetts, for example, occur in sediments with a substantially higher silt+clay (hereafter called "mud") content than similar communities in Long Island Sound, New York (Buchanon, 1963). Even within Sanders' (1958) Buzzards Bay study area, mixed trophic assemblages were observed in some sediments containing similar proportions of mud as sediments where deposit feeders dominated. These examples suggest that grain size may, in fact, be correlated with the actual causative variable(s) such that the relationship between grain size and species distribution is at least partially indirect.

Likewise, because of an increasing appreciation for the role of boundary-layer flow and sediment transport in benthic ecology, our conceptual picture of the ways in which infaunal organisms interact with sediments and the near-bed flow regime is undergoing a renaissance. Most natural-history information has been derived from observations of organisms in still water; such observations are now known to present an erroneous picture of the behaviour of many infauna that have been tested under

hydrodynamic and sediment-transport conditions that occur in the field (e.g., Taghon et al., 1980; Muschenheim, 1987a; Grizzle & Morin, 1989; Nowell et al., 1989; Turner & Miller, 1991a, b; Brandon, 1991; Miller et al., in press; Taghon & Greene, in press). The development of new technology for observing animal behaviour under simulated natural conditions in the laboratory, such as seawater flumes and wave tanks, high-speed movie cameras, low-light and high-resolution video cameras, and automated motion analysers, now permits meaningful studies of interactions between biological, hydrodynamic, and sediment-transport processes in the benthos. Likewise, continuing improvements in manned and remotely operated underwater vehicles facilitate field observations and experiments at water depths and under conditions untouchable for the study to the investigator of several decades hence.

A relatively new concept that is germane to this review is the mounting evidence for plasticity in feeding mode as a function of the flow and sediment-transport regime. Many species of surface deposit feeders, for example, are now known to be facultative suspension feeders (e.g., Hughes, 1969; Buhr & Winter, 1977; Fauchald & Jumars, 1979; Salzwedel, 1979; Dauer et al., 1981), evidently in response to flow and elevated fluxes of suspended particulates (Taghon et al., 1980; Olafsson, 1986; Thompson & Nichols, 1988; Levinton, 1991; Taghon & Greene, in press). "Switching" between deposit- and suspension-feeding can occur over a tidal cycle, as observed for the bivalve Macoma balthica (Brafield & Newell, 1961). Switching can also occur within a single, bedload-transporting flow regime, depending on the location of the organism relative to ripple geometry, as observed for the spionid polychaete Pseudopolyora kempi japonica

at slow ripple migration rates (Nowell et al., 1989). Furthermore, the extensive, detailed observations of Miller et al. (in press) of the feeding behaviour and motility of a wide variety of soft-substrate invertebrates species in a laboratory wave tank indicate various kinds of responses to oscillatory flow. These responses are correlated not simply with feeding mode, but more specifically with the functional morphology of the appendages used for particle capture. In fact, of the 16 species studied, representing five invertebrate phyla and water depths from the intertidal to the continental shelf, only one (the only burrowing species examined -- the predatory starfish Astropecten americanus) did not change feeding behaviour in response to oscillatory flow. Epifaunal gastropods also showed changes in motility with increasing oscillatory flow and sediment transport. The conventional concepts of "feeding guilds" (sensu Fauchald & Jumars, 1979) and "functional groups" (sensu Rhoads & Young, 1970) therefore must be revised to account for behaviour as a function of the flow and sediment-transport regime (e.g., Jumars & Nowell, 1984a; Nowell et al., 1989; Okamura, 1990; Shimeta & Jumars, 1991; Turner & Miller, 1991a; Miller et al., in press).

In this paper, first we critically review studies of the relationship between infaunal distributions and the grain size, organic content, micro-organisms, and "stability" (including amensalistic interactions) of sediments, aspects that were treated in past reviews and overviews on this subject (e.g., Gray, 1974, 1981; Rhoads, 1974; Pèrés, 1982; Probert, 1984). These aspects of sediments are not mutually exclusive; we use these groupings for historical reasons and emphasize the relationships among these sediment "characteristics" wherever possible. We then review existing data on two very

different infaunal species (the bivalve Mercenaria mercenaria and the polychaete Owenia fusiformis) which we have chosen to illustrate how even relatively well-studied species have distributions that are not well understood. Next we discuss processes responsible for surficial sediment distributions to provide a contemporary physical context for interpreting observed distributions of infauna and sediments. Infaunal distributions are then evaluated relative to parameters that may covary with sediment type (flow regime, sediment-transport regime, larval supply and food supply). A discussion of multidisciplinary research on Georges Bank, U.S.A., is then provided to illustrate the complex and dynamic nature of near-shore, sedimentary environments and animal-sediment relationships therein. We conclude with a discussion of the kinds of experiments and sampling needed to help clarify issues that previous correlative studies simply could not address.

The thread that is woven throughout this review is intended to highlight the importance of relationships among parameters within the soft-sediment environment. We suggest that some attempts to isolate and attribute causation to a single isolated factor have failed simply because of the strong co-variance among many variables in this environment. For example, we are perplexed by the developing discussion in the literature on suspension feeding regarding whether it is food concentration, flow velocity, or food flux that controls feeding rate and growth of benthic suspension feeders (e.g., Cahalan et al., 1989; Grizzle & Morin, 1989; Grizzle & Lutz, 1989; Emerson, 1990; Muschenheim & Newell, 1992). These factors are so strongly inter-related in nature that decomposing them makes little sense, even if it were possible to do so

experimentally (see also Fréchette et al., in press).

## ASPECTS OF SEDIMENTS TO WHICH ANIMALS MAY RESPOND

### GRAIN SIZE

Although numerous studies are cited in support of the notion that infaunal distributions are correlated with sediment grain size (e.g., Table I), most studies provide little insight regarding the mechanism(s) responsible for such associations. Furthermore, associations between animals and grain-size distributions generally have been evaluated using somewhat subjective criteria, such as comparisons of species lists among sediment habitats (e.g., Petersen, 1913; Spärck, 1933; McNulty et al., 1962a, b; Young & Rhoads, 1971), community trellis diagrams (Sanders, 1958; Sanders et al., 1962; Bloom et al., 1972) and classification analysis (Pearson, 1970a; Stephenson et al., 1970; Eagle, 1973; Ishikawa, 1989). The subjectivity of these comparisons may contribute to the degree to which different investigators have reported the strength of animal-sediment associations. Moreover, analyses that provide some form of statistical evaluation of the strength of association, such as ordination (e.g., Cassie & Michael, 1968; Hughes & Thomas, 1971; Flint & Holland, 1980) or correlation (e.g., Bloom et al., 1972) have found strong relationships in some instances (e.g. Nichols, 1970; Ishikawa, 1989; Palacin et al., 1991) but not others (Hughes & Thomas, 1971; Bloom et al., 1972; Flint & Holland, 1980). In general, these studies have shown that there are many species that are characteristically associated with a given sedimentary habitat, although their

distributions are rarely confined to that environment. Some species show little affinity with any one particular sediment type, and the fauna within different sediment environments invariably show some degree of overlap. One explanation for these inconsistencies is that grain size may be a correlate of the actual causative factor(s).

Sediment sampling has also generally reflected a lack of appreciation for the vertical position of fauna of different trophic groups within the sediment bed. Furthermore, standard grain-size analysis has always involved disintegration of natural aggregates. In the vertical, for example, grain-size distributions were invariably determined on sediments integrated over at least the top several centimetres (e.g., Table I). These grain-size distributions may be deceptive in graded beds (e.g., Rhoads & Stanley, 1965; Grant & Butman, 1987; Butman & Wheatcroft, 1991) where grain sizes encountered by organisms within a given stratum may be poorly represented in vertically mixed sediment samples (Hughes & Thomas, 1971; Grehen, 1990). Vertical partitioning of organisms in sediments is known to occur (e.g., Mangum, 1964; Rhoads, 1967; Boaden & Platt, 1971; Whitlatch, 1980; Joint et al., 1982; Palmer & Molloy, 1986) and surficial sediments available to surface deposit feeders, for example, may differ considerably in grain-size distribution and carbon content from sediments scavenged at depth in the bed by subsurface, "conveyor-belt" species (e.g., Mangum, 1964; Rhoads, 1967; Fauchald & Jumars, 1979; Butman & Wheatcroft, submitted). Likewise, processing of samples for grain-size distributions usually involved the use of a dispersant to disintegrate natural aggregates, such as fecal pellets, into primary sediment particles (e.g., Folk, 1980). Resulting grain-size distributions may not be meaningful

if the animals respond to natural, intact aggregates, rather than to primary (i.e., disaggregated) sediment particles (e.g., Jumars & Nowell, 1984a, b; Fuller & Butman, 1989).

The most compelling evidence that grain size may influence species distributions comes from small-scale (millimetres to centimetres), still-water, laboratory experiments on larval settlement. Some echinoid larvae did not settle (Mortensen, 1921, 1938) and some polychaete larvae delayed metamorphosis (Wilson, 1932, 1936, 1951; Day & Wilson, 1934) until exposed to sand or, for one species, muddy sand (Wilson, 1937). In other laboratory experiments (e.g., Table II; see also Table V in C.A. Butman, 1987) larvae or adults were given a choice of sediment treatments in small dishes and, for the most part, the organisms selected sediment that most closely resembled the adult habitat in nature (e.g., reviews of Gray, 1974; Scheltema, 1974). When the choices were restricted to different grain-size classes, larvae of several species of infaunal invertebrates (e.g., Wilson, 1948; 1952; Gray 1967a) and several species of mobile adults (e.g., Wieser, 1956; Williams, 1958; Webb & Hill, 1958; Meadows, 1964a) showed selectivity for a particular size class (Table II). There was little evidence, however, that the response was to grain size alone, and the response may have been to factors associated with the grains (e.g., organic films or microbial populations; Gray, 1974; Scheltema, 1974) or correlated with grain-size distributions (e.g., sediment "stability"; Rhoads, 1974, or the near-bed flow regime; Nowell & Jumars, 1984). Indeed, in single-species, sediment-selection experiments in laboratory flume flows, larvae of the polychaetes Capitella sp. I (Butman et al., 1988b; Butman & Grassle, 1992; Grassle

Table II. Summary table of soft sediment, substrate selection experiments. Experiments on gregarious settlement are not included, since none have established how initial colonization takes place.

| Study | Still water or flow? | Substrate Choice | Larvae or adults? | Species | Selection? Expected Choice? | Conclusions |
|---|---|---|---|---|---|---|
| Mortensen (1921) | Still water | Sand present or absent | Larvae | Mellita sexies perforata | Yes<br>Yes | Sand presence needed to metamorphose |
| Wilson (1932) | Still water | Sand to mud | Larvae | Owenia fusiformis | Yes<br>Yes | No data, but metamorphose only in fine sand, not mud |
| Day & Wilson (1934) | Still water | Sand to mud | Larvae | Scolecolepis fuliginosa | Yes<br>Yes | Faster settling in high organic muddy sand |
| Mortensen (1938) | Still water | Sand present or absent | Larvae | Prionocidaris baculosa<br>Fromia ghardaquana | Yes<br>Yes<br>Yes<br>Yes | Settlement in sand but mechanism unknown<br>As above |
| Nyholm (1950) | Still water | "Detritus film" present or absent | Larvae | Melinna cristata | Yes<br>Yes | Require non-sterile substrate to metamorphose |
| Smidt (1951) | Still water | Mud, sand, pebbles | Larvae | Pygospio elegans<br>Polydora (ligni?) | No<br>No | Settlement on all substrata but not sterile sand<br>As above but some settlement on sterile sand |
| Silén (1954) | Still water | Silty sand present or absent | Larvae | Phoronis mulleri | Yes<br>Yes | Needs "adult" habitat sand to metamosphose |
| Wilson (1955) | Still water | Treated sands | Larvae | Ophelia bicornis | Yes<br>Yes | Microbes must be present on sand for selection |
| Wieser (1956) | Still water | Grades of sand | Adults | Cumella vulgaris | Yes<br>Yes | Attracted to aged medium sediment. Food cue implied |

Table II (cont.). Summary table of soft sediment, substrate selection experiments. Experiments on gregarious settlement are not included, since none have established how initial colonization takes place.

| Study | Still water or flow? | Substrate Choice | Larvae or adults? | Species | Selection? Expected Choice? | Conclusions |
|---|---|---|---|---|---|---|
| Teal (1958) | Still water | Sand to mud | Larvae | Uca pugilator | Yes<br>Yes | Selected sand above water line |
| | | | Larvae | Uca minax | Yes<br>Yes | Selected mud above and below water line |
| | | | Larvae | Uca pugnex | Yes<br>Yes | Selected mud above and below water line |
| Webb & Hill (1958) | Still water | Coarse sand to silty sand | Adults | Branchiostoma nigeriense | Yes<br>Yes | Attracted to sand of intermediate grain size |
| Williams (1958) | Still water | Sand to sandy mud | Adults | Penaeus duorarum | Yes<br>Yes | Attracted to shell sand |
| | | | Adults | Penaeus aztecus | Yes<br>Yes | Attracted to muddy sand, sandy mud, and loose peat |
| | | | Adults | Penaeus setiferus | Yes<br>Yes | Attracted to muddy sand, sandy mud, and loose peat |
| Scheltema (1961) | Still water | Coarse & fine sands | Larvae | Nassarius obsoletus | Yes<br>Yes | Higher metamorphosis in coarse sand. No contact needed |
| Meadows (1964a) | Still water | Treated sands and muds | Adults | Corophium volutator | Yes<br>Yes | Preferred mud but only if untreated. Unable to restore attractivity |
| | | | Adults | Corophium arenarium | Yes<br>Yes | Preferred sand, only if untreated, otherwise as above |
| Meadows (1964b) | Still water | Depths of Mud | Adults | Corophium volutator | Yes<br>Yes | Chose muds where it could burrow fairly deeply |

Table II (cont.). Summary table of soft sediment, substrate selection experiments. Experiments on gregarious settlement are not included, since none have established how initial colonization takes place.

| Study | Still water or flow? | Substrate Choice | Larvae or adults? | Species | Selection? Expected Choice? | Conclusions |
|---|---|---|---|---|---|---|
| Gray (1966) | Still water | Grades of sand | Adults | Protodrilus symbioticus | Yes<br>Yes | Attractant was specific bacteria, related to grain size |
| Croker (1967) | Still water | Clean or silty sand | Adults | Haustorius sp. | Yes<br>Yes | Preferred clean sand as in nature |
| | | | Adults | Neohaustorius schmitzi | Yes<br>Yes | As above |
| | | | Adults | Parahaustorius longimerus | No | No preference. Widely distributed in nature |
| | | | Adults | Lepidodactylus dytiscus | No | As above |
| | | | Adults | Acanthohaustorius sp. | No | As above |
| Gray (1967a) | Still water | Grades of sand | Adults & larvae | Protodrilus rubriopharyngeus | Yes<br>Yes | Attracted to coarse specific bacteria was cue |
| Gray (1967b) | Still water | Grades of sand | Adults & larvae | P. hypoleucus | Yes<br>Yes | As above |
| Jansson (1967) | Still water | Grades of sand | Adults | Coelogynophora schulzii monospermaticus | No | Did not select particular grain size |
| Gray (1968) | Still water | Grades of sand | Adults | Leptastacus constrictus | Yes<br>Yes | Attractant was bacteria in larger grain sediments |
| | | | Adults | Aktedrilus | No | As above |
| Lewis (1968) | Still water | Mud to sand | Adults | Fabricia sabella | No | No preference but wide natural distribution |

Table II (cont.). Summary table of soft sediment, substrate selection experiments. Experiments on gregarious settlement are not included, since none have established how initial colonization takes place.

| Study | Still water or flow? | Substrate Choice | Larvae or adults? | Species | Selection? Expected Choice? | Conclusions |
|---|---|---|---|---|---|---|
| Sameoto (1969) | Still water | Grades of sand | Adults | Haustorius canadensis | Yes<br>Yes | Preferred coarser grains but attraction lost on combustion |
| | | | Adults | Neohaustorius biarticulatus | Yes<br>Yes | As above |
| | | | Adults | Acanthohaustorius millsi | Yes<br>Yes | Preferred medium grain sediments |
| | | | Adults | Parahaustorius longimerus | Yes<br>Yes | As above |
| | | | Adults | Protohaustorius deichomannae | Yes<br>Yes | As above |
| Gray & Johnson (1970) | Still water | Sands with bacteria | Adults | Turbanella hyalina | Yes<br>Yes | Attracted to specific bacterial cell wall compound |
| Hadl et al. (1970) | Still water | Grades of sand | Adults | Microhedyle milaschewitchii | Yes<br>Yes | Selected medium grain particles, bacterial settlement cue isolated |
| Morgan (1970) | Still water | Grades of sand | Adults | Pectenogammarus planicrurus | Yes<br>Yes | Prefer larger grains. Can't negotiate small interstices. |
| Jones (1970) | Still water | Dried sand & beads | Adults | Eurydice pulchra | Yes<br>Yes | Avoids fine grain sediment. Prefers fairly coarse grain |
| | | | Adults | Eurydice affinis | Yes<br>Yes | Avoids fine grain. No mechanism given |
| Birkeland et al. (1971) | Still water | Sand/no sand | Larvae | Mediaster aequalis | Yes<br>Yes | Sand required for settlement but polychaete species presence important |
| Gray (1971) | Still water | Grades of sand | Adults | Scolelepis fuliginosa | Yes<br>Yes | Specific bacteria restored attractiveness of sand |

Table II (cont.). Summary table of soft sediment, substrate selection experiments. Experiments on gregarious settlement are not included, since none have established how initial colonization takes place.

| Study | Still water or flow? | Substrate Choice | Larvae or adults? | Species | Selection? Expected Choice? | Conclusions |
|---|---|---|---|---|---|---|
| Phillips (1971) | Still water | Sand to mud | Adults | Callianassa islagrande | Yes? Yes | No data, claim selection preference for sand - mud clogs |
| | | | Adults | C. i. louisianensis | Yes? Yes | No data given but preferred mud...sand too hard to burrow |
| Chia & Crawford (1973) | Still water | Grades of sand | Larvae | Ptilosarcus guerneyi | No | Did not select on grain size but did need microbes |
| Keck et al. (1974) | Still water | Mud to sand | Larvae | Mercenaria mercenaria | Yes Yes | Higher settlement in sand clam "liquor" treated sand |
| Botero & Atema (1982) | Still water | Mud, rock & sand | Larvae | Homarus americanus | No | Favoured rocky bottom, also settled well on mud |
| Cuomo (1985) | Flow (crude) | Mud with sulphide varied | Larvae | Capitella sp. I | Yes? Yes | "Settled" where sulphides highest, but see Dubilier (1988) |
| Rice (1986) | Still water | Sand & silty-sand | Larvae | Golfingia misakiana | No | No substrate selection but combustion reduces attraction |
| Butman et al. (1988) | Both | Mud & beads | Larvae | Capitella sp. I | Yes Yes | Select high organic mud over sand |
| Zimmerman et al. (1988) | Still water | Sandy mud to sand | Adults | Microphiopholis gracillima | Yes Yes | Adults selected sediment they normally occur in |
| Bachelet et al. (1992) | Still water | Mud & beads | Larvae | Mercenaria mercenaria | No | No preference observed |
| Butman & Grassle (1992) | Both | Several choices of sediment | Larvae | Capitella sp. I | Yes | Selection but evidence for hydrodynamic modification |

Table II (cont.). Summary table of soft sediment, substrate selection experiments. Experiments on gregarious settlement are not included, since none have established how initial colonization takes place.

| Study | Still water or flow? | Substrate Choice | Larvae or adults? | Species | Selection? Expected Choice? | Conclusions |
|---|---|---|---|---|---|---|
| Grassle et al. (1992) | Both | Muds, sand & beads | Larvae | Capitella sp. I | Yes<br>Yes | Selection of muds over beads and sometimes sand |
| Grassle et al. (1992) | Both | Mud & beads | Larvae | Mulinia lateralis | Yes<br>Yes | Select high organic mud more consistently in flow |
| Snelgrove et al. (1993) | Both | Mud & beads | Larvae | Capitella lateralis<br>Mulinia lateralis | Yes<br>Yes<br>Yes<br>Yes | Evidence for some hydrodynamic influence of settlement<br>Evidence for strong hydrodynamic influence on settlement |

et al., 1992a; Snelgrove et al., 1993) and Capitella sp. II (Grassle & Butman, 1989) and the bivalve Mulinia lateralis (Grassle et al., 1992b; Snelgrove et al., 1993) settled differentially on two sediment treatments with similar grain-size distributions but with different organic contents. The sediment treatments also differed, however, in angularity and composition of the grains and in microbial populations.

It is difficult to extrapolate from laboratory experiments on larval settlement and correlative field studies on distributions of adults to explain the mechanisms producing natural distributions of infaunal organisms. Correlations between distributional patterns of early recruits and sediments have been interpreted both as an active response to sediment type (including grain size) and as a result of passive deposition (reviewed in C.A. Butman, 1987). The passive deposition hypothesis states that larvae are deposited onto the seabed like passive particles such that physical characteristics of the larvae (e.g., size, specific gravity and gravitational fall velocity) and the near-bed flow regime determine initial settlement sites. This mechanism explicitly accounts for correlations between infaunal and grain-size distributions because larvae and sediment grains that are hydrodynamically comparable would transport similarly in the near-bed flow (Hannan, 1984; Butman, 1989) and be deposited in similar locales on the bottom (Eckman, 1990; Gross et al., 1992). Thus, for this hypothesis, it is the flow and sediment-transport regime, not the grain size, per se, that determines the pattern.

Another mechanism that could result in sediment-specific distributions is preferential ingestion or retention of specific grain sizes during feeding. Although adults of a variety of species have been shown to ingest specific grain sizes of sediments (e.g.,

Hylleberg & Gallucci, 1975; Whitlatch, 1977, 1980; Lopez & Kofoed, 1980; Self & Jumars, 1978, 1988; Taghon, 1982; Whitlatch & Weinberg, 1982), it is unclear how this may relate to the establishment of animal-sediment associations. A number of adult deposit feeders have been shown to ingest smaller particles selectively (e.g., Taghon, 1982), but selection is not exclusive and may become less specialised in larger animals (e.g., Self & Jumars, 1988). Furthermore, larger particles may be preferred by larger animals within a given species (Whitlatch & Weinberg, 1982), and, likewise, newly settled larvae may be restricted to feeding on the finest material within the bed (Jumars et al., 1990); thus, optimal grain size may be different for settling larvae and adults. The preferential ingestion of protein-coated beads over non-coated beads observed for several deposit feeders (Taghon, 1982), and the higher organic content often, although not always (Cammen, 1982), associated with smaller (e.g., Longbottom, 1970; Hargrave, 1972; DeFlaun & Mayer, 1983) and more angular (e.g. Johnson, 1974; Whitlatch, 1974) grains, suggests that food requirements may actually be the motivating factor in selective ingestion of particular grain sizes. Habitat selection based on the availability of a preferred grain size in feeding is difficult to conceptualise, however, in view of the ontogenetic and hydrodynamic changes in feeding behaviour and particle selectivity described above. A more detailed treatment of deposit feeding as a function of sediment quality is given by Lopez & Levinton (1987) and Lopez et al. (1989).

In summary, although grain size is commonly purported to be correlated with faunal distributions, there is actually very little documentation for the mechanisms that result in the observed pattern. The fact that the relationship is sometimes weak or

variable from one habitat to the next (see Table I) suggests that other correlates may be more important. Passive deposition of settling larvae (and survival to adulthood in initial depositional locales) is one of the most parsimonious mechanisms whereby sediment grain size could be a predictor of patterns of adult distribution. If this mechanism is indeed operating, it is not grain size, per se, that determines the pattern; it is the boundary-layer flow and sediment-transport regime that ultimately determines adult distributions via passive deposition of larvae.

## ORGANIC CONTENT

The organic content of bottom sediments may be a more likely causal factor than sediment grain size in determining infaunal distributions because organic matter in sediments is a dominant source of food for deposit feeders and, indirectly (e.g., through resuspension), for suspension feeders. As Sanders et al. (1962) succinctly stated, "The sediment must be considered as an indicator of the availability of food, and not as a first order factor directly determining the distribution of feeding types." Still, of the 64 papers on animal-sediment relationships cited in Table I, 51 of which were published after Sanders' (1958) benchmark study, the organic carbon content of sediments was measured in fewer than half of them. This may reflect a realization by investigators that bulk carbon measurements may not accurately reflect the amount of carbon that may actually be utilized by an organism (e.g., Tenore et al., 1982; Cammen, 1989; Mayer, 1989; Mayer & Rice, 1992), and the potential diversity of carbon sources (Johnson, 1974). Indeed, Johnson (1974) stated, "The standard methods of describing sediment

are inadequate for understanding animal-sediment relations and geological processes." Nonetheless, a number of studies on animal-sediment relationships (e.g., Longbottom, 1970; Nichols, 1970; Field, 1971; Pearson, 1971b; Ishikawa, 1989) have suggested that there is a strong relationship not only between animal and grain-size distributions but between animals and organic-carbon distributions as well.

Perhaps the most compelling evidence that the supply of carbon influences infaunal distributions comes from pollution studies (reviewed by Pearson & Rosenberg, 1978; Gray et al., 1990; and others), which have documented dramatic faunal changes resulting from coastal eutrophication. Although increases in the carbon content of sediments does not always result in similar faunal changes, this may be, in part, a result of confounding factors such as toxic compounds, sedimentation, and changes in oxygen availability. In one study where eutrophication occurred as a result of fish farming, and was therefore not confounded by the presence of toxins, faunal changes were observed where carbon levels were elevated (Weston, 1990). Pollution studies extend beyond the scope of this review; however, given the complexity and present level of understanding of animal-sediment associations, we suggest caution in interpreting pollution studies which generate predictive equations based on assumed relationships between trophic composition, grain-size distribution, and pollution effects (e.g., Satsmadjis, 1982, 1985; Maurer et al., 1991).

Organic matter may limit distributions of organisms through differential settlement of larvae (or post-larvae) or differential post-larval survival. Unfortunately, the way in which organisms are able to utilise different types of carbon is an extremely

complex issue that we are only just beginning to understand (e.g., Lopez & Levinton, 1987). Organic matter may take many different forms (e.g., Johnson, 1974; Whitlatch & Johnson, 1974) and different forms of organic matter may be utilized in very different ways (Tenore et al., 1982). In fact, the specific components of organic matter that are of highest food value to deposit feeders is currently an area of active research (e.g., Lopez & Levinton, 1987; papers in Lopez et al., 1989; Plante et al., 1989; Carey & Mayer, 1990; Mayer & Rice, 1992) that is likely to significantly improve our understanding of why organisms live where they do. Thus, bulk measurements of carbon in correlative studies (Table I) may suggest avenues for future research but are unlikely to clarify how patterns of distribution are established and maintained. A good example of what needs to be done is the recent study of Taghon & Greene (in press) who tested the hypothesis that switching from deposit feeding to suspension feeding for two infaunal polychaete species was energetically profitable because suspended particles have greater food value. They showed that although suspended particles had greater mass-specific concentrations of total organic matter, organic carbon, labile protein, nitrogen, and chlorophyll a, both species fed at significantly lower volumetric rates when suspension feeding (evidently because of the elevated food gain per unit time when suspension feeding) than deposit feeding. Only one of the two closely related species grew as well or better on the suspended material, however, a counter-intuitive biological response underscoring the complex relationships among feeding physiology, the nature of food, and food supply.

Sanders' (1958) original hypothesis was that deposit feeders are more abundant

in muddy environments because fine sediments tend to be organic-rich. Taghon & Greene's (in press) recent measurements of the food value of deposited versus suspended sediment, however, question the simplicity of this explanation. Nonetheless, it has been suggested that because clays tend to bind organic matter, clay content (and thus organic carbon content) was one of the better predictors of faunal composition along the Northumberland Coast (Buchanon, 1963). In some cases, however, organic carbon may be more closely associated with the silt than the clay fraction of the sediment (DeFlaun & Mayer, 1983). Several deposit-feeding, opportunistic species have been shown to colonise preferentially organic-rich sediments over unenriched sediments with a comparable grain size in shallow-water (Grassle et al., 1985) and deep-sea (Snelgrove et al., 1992) environments. Adult amphipods may select sediment based on organic content, although a response to sediment roughness may also be involved (DeWitt, 1987).

Aside from the issue of quality of organic matter, there is some controversy over whether deposit feeders utilise detritus or the microbes attached to it (e.g., Levinton, 1979; Cammen, 1989), with a larger body of literature suggesting that the detritus is largely not utilised (e.g. Newell, 1965; Hargrave, 1970; Fenchel, 1970; Lopez et al., 1977). This may, however, be a function of detrital composition, since some organic matter may be more readily digestible by deposit feeders (Findlay & Tenore, 1982), perhaps in part because of the interacting effects of food quality, ciliate fragmentation of detritus, and bacterial activity (Briggs et al., 1979). Several other studies have suggested that microbial carbon alone may be insufficient to support infaunal

communities (Tunnicliffe & Risk, 1977; Cammen et al., 1978).

Because many suspension feeders depend on the horizontal transport of organic matter, their distributions may be confined to areas of relatively high fluid flux (e.g., Sanders, 1958; Wildish, 1977); such high-flow areas also tend to be dominated by relatively coarse, low-organic sediments. Rates of suspension feeding and growth are a function of food supply in a variety of taxa (e.g. Muschenheim, 1987b; Grizzle & Morin, 1989; Grizzle & Lutz, 1989; Peterson & Black, 1991; Turner & Miller, 1991b), and this clearly could influence distributions of organisms. However, the addition of silt to the diets of several suspension-feeding bivalves enhanced growth (Winter, 1976; Ali, 1981; Mϕhlenberg & Kiϕrboe, 1981), probably through adsorption of dissolved organic matter onto clay particles. Resuspension of bottom material may augment phytoplankton as food for some suspension-feeding bivalves (Grant et al., 1986, 1990), although other species have shown decreased growth in relatively high turbidity (Bricelj et al., 1984; Murphy, 1985; Grizzle & Lutz, 1989; Huntington & Miller, 1989; Turner & Miller, 1991b). Moreover, as discussed earlier, suspension feeding is not necessarily limited to those animals living in relatively coarse sediments. A number of deposit feeders living in muddy sediments suspension feed in response to suspended sediment flux (e.g., Taghon et al., 1980; Levinton, 1991), and some species once thought to be suspension feeders actually utilise deposited sediment as well (e.g., Mills, 1967; Tenore et al., 1968; Hughes, 1969). Thus, given the complex relationship between feeding mode and the organic content of the sediment, generalising about feeding mode and sediment organic content is, at present, a risky proposition.

Controlled, laboratory experiments on larval settlement suggest that preference for a given grain size may be related to organic content and that the pattern may be determined, at least for some species, by differential settlement rather than by post-settlement survival. A detrital coating was apparently necessary to induce settlement of ampharetid polychaetes (Nyholm, 1950), and variation in sediment organic content influenced sea pen settlement (Chia & Crawford, 1973). Related studies on microflora are summarised separately (see next section). In flume and still-water, single-species experiments using sediments with similar grain-size distributions but varying widely in organic content (and also in microbial abundances and in the angularity and composition of the sediment particles), more larvae settled in the high-organic treatments for the three species that live in organic-rich sediments as adults (Butman et al., 1988b; Butman & Grassle, 1992; Grassle et al., 1992a, b), but settlement was non-selective for a species with low habitat affinity as adults (Bachelet et al., 1992).

Clearly, many infaunal organisms respond to organic matter, both actively and passively, and as larvae, juveniles, and adults. Current issues concerning the quality, as well as the quantity, of organic matter as food for both deposit and suspension feeders, plasticity in feeding mode, the specificity of feeding types to sediment types, and boundary-layer flow regime as a covariant of sediment type (discussed more later) render premature the development of a unifying principle regarding the organic content of sediments as the causal factor determining patterns of infaunal distributions.

## MICRO-ORGANISMS

The relatively large surface area of fine sediments undoubtedly contributes to the higher microbial activity observed in fine relative to coarse sediments (e.g., Newell, 1965; Cammen, 1982; Yamamoto & Lopez, 1985), and infaunal response to microbial populations could result in specific animal-sediment relationships. Growth rates of the microbial food of deposit feeders may also be dependent on grain size (e.g. Taghon et al., 1978; Doyle, 1979; Cammen, 1982), perhaps through effects of porosity on nutrient flux through the sediment (e.g. Bianchi & Rice, 1988).

Depending on the organisms involved and the source of organic matter, microbial populations may be the dominant source of nutrition for deposit feeders living in muddy sediments. It has been suggested that some infaunal species, such as the polychaete Nereis succinea, obtain a portion of their nutrition from microbes and the remainder from plant detritus (Cammen, 1980). Other species, such as Capitella "capitata", may utilise microbes on refractory plant detritus such as marsh grass, but rely more on the plant detritus itself when it is easily digestible (e.g. Findlay & Tenore, 1982). Elevated bacterial activity and growth in the feces of benthic detritivores (Fenchel, 1970, 1972; Hargrave, 1970; Juniper, 1981; Newell, 1965) may quickly replenish a depleted food resource; however, selective pressure would tend to favour foraging strategies that minimize the probability of re-ingestion of fresh (i.e., microbially depleted) feces (e.g., Miller & Jumars, 1986; Miller et al., 1984), as demonstrated also for the deposit-feeding polychaete Amphicteis scaphobranchiata (Nowell et al., 1984).

Deposit feeders living in sandy environments, however, can probably satisfy only a minor portion of their nutritional requirements with sedimentary bacteria alone (e.g.,

Plante et al., 1989). Low microbial biomass is well documented in sandy sediments (e.g., Meadows & Anderson, 1968; Steele & Baird, 1968; Steele et al., 1970; Weise & Rheinheimer, 1978; de Jonge, 1985; de Jonge & van der Bergs, 1987) and has been attributed to abrasion effects in this highly dynamic sediment-transport environment (e.g., Munro et al., 1978; DeFlaun & Mayer, 1983; Miller, 1989). Thus, the microbial content of sands is probably not important as a food source, but this does not necessarily suggest that the microbial flora of sand is unimportant to colonizing fauna.

A number of studies have suggested that microbial biomass in marine sediments influences the distribution of adult infauna. Laboratory experiments, for example, indicate that meiofauna respond to differences in bacterial availability (Gray, 1966, 1967a, 1968). Field population densities of the gastrotrich Turbanella hyalina were correlated with a bacterial species having a particular type of cell wall, and still-water selection experiments suggested that the gastrotrichs actively selected sediments containing this bacterium (Gray & Johnson, 1970). Harpacticoid copepods have also been shown to respond actively to microbial enrichment in field experiments (Kern & Taghon, 1986), and partitioning of bacterial and phototrophic resources is important in the coexistence of three species of benthic copepods (two harpacticoids and one cyclopoid) (Carman & Thistle, 1985). Several meiofaunal species have been shown to respond to microbially-enriched sediments in field and laboratory experiments (Kern, 1990), the proposed mechanism being differential migration following passive settlement. Furthermore, biological structures in sediments, such as tubes and seagrass shoots, enhance the local boundary shear stress and fluid flux to the bed (Eckman &

Nowell, 1984). Enhanced nutrient flux apparently leads to increased bacterial biomass near the structure (Eckman, 1985) resulting, for example, in local increase of harpacticoid copepod densities (Thistle et al., 1984). A number of studies have found elevated bacterial and metazoan densities around burrows (e.g., Hylleberg, 1975; Aller & Aller, 1986; Reise, 1987), although the mechanism(s) involved were not clearly identified. Moreover, stimulation of microbial growth by feeding and irrigation ("microbial gardening") may be a mechanism by which deposit feeders increase their own food supply (e.g., Hylleberg, 1975; Miller et al., 1984; Grossmann & Reichardt, 1991). Finally, the presence of micro-organisms, rather than a given physical characteristic of the sediment, has been shown to induce larval settlement in several infaunal species (e.g., Smidt, 1951; Wilson, 1955; Scheltema, 1961; Gray 1967a; see also reviews of Gray, 1974; Scheltema, 1974).

Thus, the microbial community is a potentially important aspect of bottom sediments, particularly as a food supply to deposit feeders in muds, and may influence infaunal distributions. In a more detailed review of the role of microbes as food for deposit feeders, Lopez & Levinton (1987) conclude, however, that only in intertidal mudflats, where benthic microalgae are extremely abundant (Cammen, 1982), would microbial food alone satisfy nutritional requirements. Moreover, microbial activity is only a crude correlate of sediment type and recent studies of interactions between microbial growth and deposit feeders (e.g., Jumars et al., 1989; Plante et al., 1989; 1990), as well as boundary-layer flow and sediment-transport effects on microbial populations (e.g., Miller et al., 1984; Grant et al., 1986a, b; Grant & Gust, 1987; Miller,

1989; Dade et al., 1990), suggest that understanding the factors that control the distribution, growth rates, and biomass of sediment micro-organisms will continue to be an important and complex subject of future studies.

## "STABILITY" AND AMENSALISM

Sediment "stability" has been defined in a number of different ways throughout the years. In benthic ecology, the concept may have been launched by Fager's (1964) observation that an unusually dense assemblage of the tube-building polychaete Owenia fusiformis and the burrowing anemone Zaolutus actius "had a profound stabilising effect on the bottom sediment" in a shallow, sandy region of La Jolla Bay, California. Physical evidence for a local, stabilised substrate within this sandflat was the lack of ripple formation and resuspension in the worm-tube bed. Biological evidence of stabilisation included presence of other animals that "would appear to require a stable substrate" and that did not occur elsewhere on the sandflat, as well as growth of a diatom film normally found at deeper depths where there was considerably less wave surge activity. Fager (1964) did not speculate on the mechanism by which the bed was stabilised, but recent laboratory flume experiments suggest that stabilisation was probably due to mucous-binding of the sediments, rather than to a purely hydrodynamic "skimming flow" effect (Eckman et al., 1981, 1985). Numerous field studies (e.g., Galtsoff, 1964; Mills, 1967; Young & Rhoads, 1971; Daro & Polk, 1973; Bailey-Brock, 1979; McCall & Fisher, 1980) document similar observations of dense concentrations of a variety of surface-evident biological structures, such as seagrass shoots and animal

tubes, that purportedly produce sediment-stabilising effects similar to, although perhaps not as dramatic as, those observed by Fager (1964). However, none of these studies delineated the objective or quantitative criteria by which "stability" was assessed (sensu Nowell et al., 1981; Grant et al., 1982; Jumars & Nowell, 1984a).

It was the experimental field study of Rhoads & Young (1970), and their novel interpretation of their results in terms of "amensalistic interactions" (discussed below) that introduced to benthic ecologists the concepts of classifying sediments as "stable" or "unstable" and benthic assemblages as "stabilising" or "destabilising". Based on the premise that deposit feeders tend to dominate muddy sediments and suspension feeders tend to dominate sandy sediments, Rhoads & Young (1970) proposed that sediment reworking by deposit feeders in muddy sediments increases resuspension and thus excludes suspension feeders by inhibiting filtering activity and burying larvae. They called this the "trophic group amensalism" hypothesis. (Note that the original hypothesis explains only the exclusion of suspension feeders from muddy habitats). Like Sanders (1958) and Sanders et al. (1962), Rhoads & Young (1970) argued that deposit feeders are poorly represented in sandy areas because of an inadequate food supply due to the high rates of horizontal sediment flux (advantageous for suspension feeders) and low rates of deposition of organic matter. Support provided by Rhoads & Young (1970) for trophic group amensalism in Buzzards Bay, Massachusetts were observations of increased water content and erodability of sediments reworked by deposit feeders, and reduced growth rates of the suspension-feeding bivalve Mercenaria mercenaria when transplanted close to the bottom in a muddy habitat.

Rhoads and Young's field study represented one of the first attempts to determine experimentally the underlying mechanism for observed animal-sediment associations. Unfortunately, their research tended to stimulate an even more concentrated effort to quantify animal distributions in relation to sediment characteristics rather than promoting more experimental tests of hypotheses to explain such correlations. This was particularly unfortunate because of several major shortcomings in the study of Rhoads & Young (1970). For example, they provided no direct evidence for the burial of larvae of suspension feeders in muddy sediments, or of food limitation of deposit feeders in sandy sites. Furthermore, Dayton & Oliver (1980) later pointed out that whereas growth rates of Mercenaria mercenaria were lower in Rhoads and Young's (1970) transplants just above the muddy bottom, compared to transplants suspended higher in the water column, the near-bottom animals still had growth rates similar to those of animals in the sandy controls. Dayton & Oliver (1980) suggested that enhanced growth with distance above the muddy bottom may be due to higher rates of horizontal food flux because flow speed increases with distance above the bed.

The concept of classifying organisms as "functional groups" that either stabilise or destabilise bottom sediments was refined and developed further in Rhoads' (1974) review, but these concepts can be legitimately criticised on several fronts. First, there is very little evidence (discussed earlier) for the generalisation that deposit feeders are restricted largely to muddy sediments and suspension feeders to sandy sediments. Furthermore, given recent observations of feeding and mobility of infauna under realistic flow and sediment-transport regimes (see previous section), categorising infaunal

organisms into simple functional groups such as deposit or suspension feeders, irrespective of the hydrodynamic and sediment-transport regime, is no longer meaningful. Sanders (1958), for example, originally suggested that almost 66% of the individuals in his typical "sand community" were suspension feeders and over 80% of the fauna in his typical "mud community" were deposit feeders. Using updated information on the feeding biology of his characteristic species (Table III), we find that approximately 62% of the dominant infauna (those species comprising >1% of total infauna, which represent approximately 48% of total individuals) in the mud community were deposit feeders. The sand community, however, contained 65% deposit feeders and only about 12% suspension feeders (of the species that comprised >1% of total infauna, which represents 46% of total individuals). Furthermore, of the twelve "suspension feeders" characterizing Sanders' sandy habitats, only two are now unequivocally accepted as feeders on suspended material.

There are other studies correlating trophic groups with sediment type that have, in our estimation, also found no clear relationship. Pearson (1971), for example, divided fauna into a number of groups, including suspension feeders, surface deposit feeders and deposit "swallowers", and found a significant positive correlation between surface deposit feeders and the silt content of the sediment. There were no significant correlations, however, between suspension feeders or deposit "swallowers", and any of the sediment parameters that he measured. In the study of Bloom et al. (1972), densities of suspension and deposit feeders were not significantly correlated with mean particle size of the habitat. The density of deposit feeders was significantly negatively

Table III. A reevaluation of distribution of feeding types in sandy and muddy habitats in Sanders' (1958) original study. Groupings are based on recent sources where behavioral observations were made. In many instances, the source for Fauchald & Jumar's (1979) conclusions was Sanders (1958) or Sanders et al., 1962), however the more recent source discusses feeding in the context of other studies on related species. Sanders suggested that the "suspension feeding" community was comprised of >66% filter feeders and the "deposit feeding" community was comprised of >80% deposit feeders.

| Dominant species in Sanders "Deposit feeding" mud community | | | | | Dominant species in Sanders "suspension feeding" sand community | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Species | Percent of Total | Suspension Feeder? | Deposit Feeder? | Source | Species | Percent of Total | Suspension feeder? | Deposit feeder? | Source |
| Nucula proxima[3] | 23.83 | | X | Lopez & Cheng (1983) | Ampelisca spinipes | 18.59 | | X[2] | Mills (1967) |
| Nephthys incisa | 17.13 | | X[1] | Fauchald & Jumars (1979) | Byblis serrata[3] | 11.31 | Flow dependent | | L. Watling (pers. comm.) |
| Turbonilla sp.[3] | 9.21 | Unable to determine | | | Cerastoderma pinnulatum[3] | 10.17 | X | | Swanberg (1989) |
| Nerinedes (=Scolelepis sp.7)[3] | 6.85 | Flow dependent, mostly suspension | | Dauer (1983) | Ampelisca macrocephala | 6.31 | | X | Mills (1967) |
| Retusa caniculata[3] | 6.00 | Predator[3] | | Berry & Thomson (1990) | Glycera americana | 5.47 | | X[1] | Fauchald & Jumars (1979) |
| Cylichna orzya[3] | 4.56 | Predator[1] | | Shoeman & Nybakken (1978) | Nephthys bucera[3] | 4.47 | | X[1] | Fauchald & Jumars (1979) |
| Ninoe nigripes | 3.01 | | X[1] | Fauchald & Jumars (1979) | Tellina tenera[3] | 3.29 | | X | Levinton (1991) |
| Ampelisca spinipes | 2.92 | | X[2] | Mills (1967) | Ninoe nigripes | 2.97 | | X[1] | Fauchald & Jumars (1979) |
| Unciola irrorata[3] | 1.85 | Flow dependent | | L. Watling & L. Schaffner (pers. comm.) | Lumbrinereis tenuis | 2.69 | | X[1] | Fauchald & Jumars (1979) |
| Lumbrinereis tenuis[3] | 1.52 | Predator | | Fauchald & Jumars (1979) | Nephthys incisa | 1.99 | | X[1] | Fauchald & Jumars (1979) |
| Tharyx acutus[3] | 1.08 | | X | Fauchald & Jumars (1979) | Unciola irrorata[3] | 1.65 | Flow dependent | | L. Watling & L. Schaffner (pers. comm.) |
| | | | | | Molgula complanata?[3] | 1.85 | X | | Bingham & Walters (1989) |
| Proportion of Each Feeding Type | | 0 | 47.97 | | | | 12.02 | 45.78 | |

[1]Closely related species are known to be predacious, so classification as deposit feeders is tentative.

[2]Feeding is somewhat intermediate in that the animal resuspends and then ingests sediment. Nonetheless, deposited, rather than horizontally transported organic matter is presumed to be the dominant food source.

[3]Conclusions on feeding mode were drawn from observations on closely related species. We were unable to find data on feeding in the species in question.

correlated with the density of suspension feeders, but the correlation was weak ($r = -0.41$). A stronger negative correlation was observed between percentage of the total fauna that were suspension versus deposit feeders ($r = -0.825$), but this is to be expected because the sums of the percentages of these two feeding types must be close to one. Another example of co-occurring deposit and suspension feeders is Peterson's (1977) study of infaunal communities in Mugu Lagoon, California, where although suspension feeders were five of the six numerically abundant species in the sand community, they were also four of the five numerically abundant species in a muddy-sand community and three of the five numerically abundant species in a mud community. In all three communities, other numerically dominant species were deposit feeders. Thus, there is good evidence from a variety of habitats that different trophic modes can co-occur in large numbers, and that distributions of suspension and deposit feeders are not mutually exclusive.

The second problem with classifying organisms as stabilisers or destabilisers is that there is little evidence for the generalisation that muddy sediments are detrimental to larval and adult suspension feeders. For example, in Hines et al.'s (1989) study of the effects of high densities of a suspension-feeding bivalve (Mya arenaria) and a "deposit-feeding" bivalve (Macoma balthica) on colonising macrofauna there was no consistent pattern relative to functional groups (i.e., they did not find, for example, negative impact of M. balthica on colonising suspension feeders). This could be a result of the fact that M. balthica has long been known to also feed on suspended material (e.g., Brafield & Newell, 1961), and although Hines et al. (1989) acknowledge this

feeding behaviour, its potential effect on experimental results was not discussed. Theoretical survivorship curves constructed from size-frequency histograms of dead shells of bivalves collected in Long Island Sound, Connecticut suggested very high juvenile mortality of the suspension-feeding bivalve Mulinia lateralis in muddy sediments (Levinton & Bambach, 1970), but this result is difficult to interpret because curves were not also constructed for shells collected from sandy habitats. Curiously, Levinton & Bambach (1970) said that this species "seems to prefer muddy habitats in New England waters", but argued that this may be due largely to high larval availability. In fact, dense populations of this opportunistic species frequently occur in organic-rich, low-oxygen situations (Stickney & Stringer, 1957; Jackson, 1968; Levinton, 1970; Boesch, 1973; Boesch et al., 1976; Holland et al., 1977; Virnstein, 1977; Rhoads et al., 1978a; Reid, 1979; Walker & Tenore, 1984a; Oviatt et al., 1984), and larvae actively select organic-rich muds over low-organic alternatives in still water and laboratory flume flows (Grassle et al., 1992b). Sediments dominated by mud, however, have a negative effect on growth rates of adults of the filter-feeding bivalve Rangia cuneata (Tenore et al., 1968). In contrast, eggs and larvae of the suspension-feeding bivalve Mercenaria mercenaria exposed to various concentrations of silt showed enhanced growth at low concentrations, but death occurred at high concentrations (Davis, 1960). Growth rates of juvenile M. mercenaria were slower under conditions of high silt concentrations (Bricelj et al., 1984). Pratt & Campbell (1956) also found reduced growth of adult M. mercenaria in trays of mud relative to adjacent trays of sand placed in the field. In none of these studies, however, was the presence of deposit feeders required to reduce growth.

Furthermore, a reduction in growth rates in muddy compared to sandy habitats does not necessarily explain the absence of an organism from the sand.

Third, in studies where trophic-group amensalism was invoked to account for the results, other explanations were equally likely, as indicated in our earlier discussion of Rhoads & Young's (1970) experiments. Another example is the distribution of suspension-feeding corals in a Jamaican coastal lagoon (Aller & Dodge, 1974), where regions with low numbers of suspension feeders were attributed to high sediment resuspension that supposedly inhibited settlement and growth. They also provided the alternative explanation that it was zooxanthellae production (e.g., see Goreau, 1961), not the corals per se, that were negatively affected by high water turbidity.

The trophic-group amensalism hypothesis has been extensively modified and qualified to explain various observations, particularly in cases where deposit feeders and suspension feeders coexist. The coexistence of suspension and deposit feeders in Cape Cod Bay, Massachusetts, for example, was attributed to unusually high tolerance of the suspension feeders to turbidity (Young & Rhoads, 1971) and to the spatial scale of bioturbation effects (Rhoads & Young, 1971). They proposed that feeding activities of the deposit-feeding holothurian Molpadia oolitica create unstable depressions, but that the fecal cones built by this species stabilise sediments in which suspension feeders may survive. This, they argued, would result in small-scale favourable and unfavourable areas for suspension feeders within a muddy habitat. Fecal cones, however, would provide little refuge from sediment resuspended from adjacent sediments without cones and would also elevate the suspension feeders into a faster flow where they may receive

enhanced horizontal food flux (e.g., Dayton & Oliver, 1980). Stabilisation of sediment by polychaete tube mats was also proposed as a means of allowing functional-group coexistence (Young & Rhoads, 1971). Moreover, an invasion of suspension feeders into a muddy habitat following an oil spill was attributed to sediment stabilisation by the oil, and subsequent mass mortality of these suspension feeders was attributed to destabilisation of the sediment as the oil dissipated (Rhoads & Young, 1970). Similarly, coexistence of suspension-feeding sabellid polychaetes and a variety of deposit feeding polychaetes in a Jamaican lagoon was attributed to the presence of binding algae or protective corals (Aller & Dodge, 1977). Likewise, enhanced recruitment of Sanguinolaria nuttallii (a suspension-feeding bivalve) in the absence of Callianassa californiensis (a deposit-feeding ghost shrimp) in Mugu Lagoon, California, was attributed to trophic group amensalism (Peterson, 1977), although he also acknowledged that suspension and deposit feeders co-occurred in large numbers in some of the sites sampled and that more complex species interactions were necessary to explain the patterns observed. Finally, Myers (1977) invoked the trophic-group amensalism hypothesis to explain the absence of suspension-feeding bivalves from a sandy (not muddy!), coastal lagoon in Rhode Island due to intense mechanical agitation of the near-surface sediments by the resident fauna. There were, however, a few abundant suspension feeders at the site, which were tubiculous, "stabilising species" that Myers (1977) claimed could persist only when fish predators were absent and water temperature was low.

These examples clearly compromise the generality of the concept of trophic-

group amensalism. In fact, one of the few studies to experimentally test an aspect of this hypothesis showed that resuspension, simulated by sediment additions to aquaria, reduced survivorship in several tube-building, deposit feeders (Brenchley, 1981). Tube builders were also negatively affected by mobile deposit feeders and mobile suspension feeders, suggesting that mobility was more important than trophic group in structuring benthic communities. High-density assemblages of tube builders may prevent the establishment of burrowers that could destabilise the sediment (Woodin, 1974; but see also criticisms of the interpretation of Woodin's results, based on subsequent experiments, in Dayton & Oliver, 1980), whereas low-density assemblages would be more susceptible to colonisation, and thus, sediment destabilisation by burrowers. Additional support for mobility-group amensalism is lacking, however, except where the mobile organism is much larger than the sedentary organisms (Posey, 1987). Survivorship of a sedentary, tubiculous polychaete (Streblospio benedicti), for example, was unaffected by a subsurface, deposit-feeding oligochaete (Monopylephorus evertus), although growth rates of S. benedicti were somewhat reduced (McCann & Levin, 1989).

The trophic-group amensalism hypothesis provides generalisations regarding animal-sediment relationships not at the population or species level of organization, but at the level of functional groups of organisms. The concept of functional groups relative to organism effects on sediments is problematic, however, because it is often difficult to categorise the effects of a given species as either sediment stabilising or destabilising (Jumars & Nowell, 1984a). A species can have more than one effect on the sediments, as suggested by Rhoads & Young (1971) for Molpadia oolitica (discussed earlier).

Moreover, even when effects of individual organisms within a community are tested separately, and rigorous criteria are used to evaluate their effects on the boundary-layer flow and sediment-transport regime (Nowell et al., 1981; Rhoads & Boyer, 1982), it is the holistic effect of the entire benthic community that determines whether sediments are more or less susceptible to transport than they would be in the absence of the fauna, flora, and microbiota (Grant et al., 1982).

Furthermore, sediment "stability", in most cases, has not been defined using physical criteria or even objectivity. Rhoads (1974), for example, refers to muddy bottoms as being "unstable" due to the sediment-reworking activities of deposit feeders. Yet, by definition, muddy bottoms are generally depositional areas that, in the absence of biological effects, are in equilibrium with much lower boundary shear stresses than sandy bottoms. Using physical criteria for "stability" based on $\tau_{cr}$, the boundary shear stress required to initiate particle motion, muds are unstable relative to sands (e.g., Shields, 1936; Miller et al., 1977) if flow conditions in the sedimentary habitats are comparable. Some biological effects, such as mucous-binding, would tend to increase $\tau_{cr}$ (e.g., Mantz, 1977; Self et al., 1989; Dade & Nowell, 1991), and others, such as pelletization and direct burial would tend to decrease the supply of fine sediments to the water column (Jumars et al., 1981). Storm events would tend to erode and transport far more sediment in a muddy habitat than in a sandy environment. The physical effect evidently referred to by Rhoads (1974) was the relative amount of sediment in suspension, which is generally higher above a muddy than a sandy bottom, and the highly mobile "fluff" layer characteristic of many bioturbated beds (e.g., Rhoads &

Boyer, 1982; Beier et al., 1991; Stolzenbach et al., 1992). Interestingly, this is a definition based more on water-column than bed characteristics, and has contributed to confusion in the literature concerning stability of sediment beds.

In summary, physically meaningful and consistent definitions generally have not been used by benthic ecologists for the terms "stable" and "unstable" with regard to bottom sediments. In addition, the formation of simple, functional groups of organisms based on still-water observations of feeding or mobility is no longer meaningful; if the concept of functional groups is to be useful, it must include considerations of organism behaviour within the context of the flow and sediment-transport regimes in which they reside. Finally, there is very little concrete support for the trophic-group amensalism hypothesis as a rigorous explanation for animal-sediment associations, and the tenet has been sufficiently compromised and modified to account for so-called "special" cases that it is now so general an explanation that it is not very ecologically meaningful.

## TWO CASE STUDIES

The complexity of animal-sediment associations, and the intimate relationship among the various factors that may produce them, can be illustrated by summarising current information on the distributions of two relatively well-studied infaunal species and the factors that may determine these distributions. The bivalve Mercenaria mercenaria was chosen because it was one of the key species studied by Rhoads & Young (1970) in the formulation of their trophic-group amensalism hypothesis, and there is a relative wealth

of both distributional and experimental studies on this organism because of its commercial importance. The polychaete Owenia fusiformis was chosen because it is relatively well-studied for a non-commercial species, and provides an interesting contrast to M. mercenaria in terms of feeding ecology (O. fusiformis has been known to switch between deposit and suspension feeding depending on flow conditions). Furthermore, O. fusiformis has been studied largely for the purpose of understanding its potential stabilising effects on sediments, as opposed to the alternative (i.e., the effects of sediment "stabilisation" on its distribution).

## MERCENARIA MERCENARIA

The hard clam Mercenaria mercenaria (hereafter called Mercenaria) is probably the most well-studied infaunal, suspension-feeding bivalve in terms of its distribution and ecology, including a large number of both observational (i.e., field distributions) and experimental (lab and field) studies. It came to be considered a classical infaunal suspension feeder that is restricted to relatively coarse sediments following Rhoads & Young's (1970) transplant experiments (described earlier) to test their trophic-group amensalism hypothesis. In this study, Rhoads and Young also quantified the abundances of suspension and deposit feeders relative to sediment type along two transects in Buzzards Bay, and although they mentioned several species of deposit feeders that dominated the muddy sites, they did not provide species-specific information for the so-called suspension-feeding communities at the sandier sites. The station locations were not far, however, from some of Sanders' (1958) Buzzards Bay transects, so we might

assume that there would be similar species or genera of suspension feeders in the two studies. If this was so, then, interestingly, Mercenaria probably was not a species dominant at any of Rhoads and Young's sandy sites because this species was not mentioned at all by Sanders (1958). Furthermore, as we pointed out previously, few of the species Sanders classified as suspension feeders in the late 1950's would still be classified as such today (Table III), and thus Rhoads & Young's sandy sites may have likewise contained very few species that were actually suspension feeders. We will return to the issue of sediment-specificity of suspension feeders like Mercenaria at the end of this section.

Assuming, for the moment, that Mercenaria mercenaria is less successful in muddy than sandy environments, then according to the trophic-group amensalism hypothesis, this distribution may be attributed to the reworking activities of deposit feeders in muds effecting lower growth rates and/or high mortality of suspension-feeding juveniles (Rhoads & Young, 1970). Furthermore, according to Sanders (1958), suspension feeders should be preferentially associated with sandy sediments because of the relatively high horizontal flux of suspended food in these environments. If there has been strong selective pressure for confinement of suspension feeders to coarse sediments, then Mercenaria larvae might be expected to select actively for sandy sediments.

The relatively long-lived (several weeks), planktotrophic larvae of Mercenaria do not appear to require a specific sediment cue to induce metamorphosis, and in the laboratory will settle on a variety of substrates, including sediments, plastics, glass, etc.

(Loosanoff & Davis, 1950). Laboratory experiments by Carriker (1961) indicated that newly recruited juveniles (byssal plantigrade stages) tended to settle on sediment with particle sizes smaller than their own shells, as opposed to coarser substrata, and that they preferred organic-rich, fine sediment. In 2-d, still-water experiments, Keck et al. (1974) found, however, that Mercenaria larvae preferred sand over mud. But, given the relatively long duration of their experiments, it is unclear whether this pattern reflected larval selectivity (i.e., initial settlement) or post-settlement redistribution. We suspect the latter, given results of the very short-term (4 h), still-water experiments of Bachelet et al. (1992), where larvae showed no sediment preference. (Note that Bachelet et al. (1992) also re-evaluated the earlier, still-water experiments of Butman et al. (1988b), where there was active selection by Mercenaria larvae for a low-organic over a high-organic sediment in still water. Because of a potential problem with preservation of the larval shell in the high-organic treatment in that study, and because Bachelet et al. attempted to replicate precisely the methods used by Butman et al. (1988b) and found no statistically significant selection, Bachelet et al. (1992) concluded that Mercenaria larvae must be considered non-selective, at least over 4 h in still water.) Butman et al. (1988b) also demonstrated very low settlement and no active selection by Mercenaria larvae in a slow, turbulent flume flow.

If Mercenaria larvae do not actively select sandy over muddy sediments at settlement, then perhaps the pattern results from enhanced passive larval supply to sandy over muddy habitats, or to differential post-settlement survival. In nature, higher densities of young and old individuals of Mercenaria have been observed in silty sand

within seagrass beds compared with purer sand in adjacent "bare" sandflats (Peterson et al., 1984; Irlandi & Peterson, 1991). Peterson (1986) compared size-frequency distributions of Mercenaria in a seagrass bed and a bare sand area and found that essentially all sizes of Mercenaria were more abundant in the seagrass bed, but the pattern was amplified in the larger size classes. Thus, the pattern may have been established at settlement (although newly settled larvae were not sampled in this study) and was subsequently enhanced via post-settlement processes (e.g., differential survival or migration due to competition or predation). The depositional environment of the seagrass bed, which results in passive accumulation of silt particles, may also passively accumulate larvae, whereas currents may be sufficiently strong to preclude high settlement in more exposed sandy areas. Thus, passively settling larvae should accumulate in higher numbers in areas of relatively low boundary shear stress, and not in the high shear stress regimes that typically characterize sandy sites. To resolve this apparent ambiguity, Pratt (1953) suggested that Mercenaria larvae settle passively in local micro-depositional sites created by rocks and shells protruding from an otherwise flat substratum. Supporting this hypothesis, Carriker (1961) observed that plantigrades (and adults) were often concentrated around, and with their byssal threads attached to, shells projecting above the bottom.

To our knowledge, there is no information on larval supply and post-settlement distribution of this species in the field, although many of the bivalves sampled by Wilson (1990) may have been Mercenaria because adults of this species are abundant in similar habitats nearby (Peterson et al., 1984; Peterson, 1986; Irlandi & Peterson,

1991). Using traps largely buried within the bed and that were designed to collect settling or resuspended larvae, Wilson (1990) collected, on average, about 50% more bivalves inside a seagrass bed than in the adjacent sandflat. At times of high larval availability, he also collected significantly higher numbers of post-larvae in the seagrass bed than in the sandflat. This suggests that settlement may determine the pattern of higher abundances in the seagrass bed, either through active habitat selection or passive deposition. Wilson's study was not designed to distinguish between these alternative hypotheses, but sediment volume collected was actually higher in traps located in the sandflat than those located in the seagrass bed, making passive deposition doubtful. If Mercenaria was the dominant bivalve species sampled by Wilson (1990), and if the seagrass bed that he studied was a local, depositional site for silts as demonstrated for a nearby seagrass bed (Peterson et al., 1984), then Wilson's results also refute preferential selection of relatively sandy sediments by settling larvae.

The issue of differential growth or post-settlement survival under conditions of high versus low suspended silt concentration that characterize muddy versus sandy habitats, respectively, has been relatively well-studied for larvae and adults, but not juvenile Mercenaria. Laboratory studies on the effect of resuspended silt on larvae indicate that levels of turbidity less than 750 mg $l^{-1}$ may actually enhance growth of larvae, although decreased growth was observed at concentrations greater than 1 g $l^{-1}$ (Davis, 1960). Even at silt levels of 4 g $l^{-1}$, however, Davis (1960) observed no significant larval mortality. Likewise, for suspended sediment concentrations of 0, 56, 110, 220, 560 and 2200 mg $l^{-1}$, Huntington & Miller (1989) could detect no differences

in larval survival, and growth was significantly reduced only at the highest silt concentration tested. It is possible that settled juveniles are more sensitive to suspended silt than are planktonic larvae, given that reduced growth of juveniles was observed at silt concentrations of only 44 mg $l^{-1}$, but not at 25 mg $l^{-1}$, in one study that was conducted on juvenile Mercenaria (Bricelj et al., 1984). Thus, there could be a recruitment "bottleneck" in high suspended silt environments. The significance of these laboratory results to natural populations is unclear, however, given that the highest silt levels observed within 3 m of the bottom in a "silt-clay basin" containing deposit feeders were only 10-35 mg $l^{-1}$ (Rhoads, 1973). Likewise, Grizzle & Lutz (1989) measured concentrations of suspended inorganic particulate matter of 51-111 mg $l^{-1}$ over sediments ranging from mud to sand, and known to contain adult Mercenaria. In the Indian River Bay, Delaware, where Mercenaria is abundant, Huntington (1988) measured suspended sediment concentrations of 10-570 mg $l^{-1}$, with an average of about 60 mg $l^{-1}$. Thus Mercenaria, at least in these cases, appears to be widely distributed with respect to suspended sediment concentration.

Data on growth rates of adult Mercenaria are somewhat inconsistent among studies. In cases where adult growth rates were compared in adjacent sandy and muddy plots, lower growth rates were found in the finer sediment treatment in some instances (Pratt, 1953), but not in others (Kerswill, 1949; Grizzle & Morin, 1989). The sandy and muddy plots in Pratt's (1953) study were both situated within a muddy habitat, however, and thus it seems likely that resuspension from the ambient, muddy sediment would have a comparable impact on both treatments. This suggests that it is some component

of the bottom sediment and not the sediment in suspension that conferred lower growth rates in Pratt's muddy plots. In contrast, Pratt & Campbell (1956) found faster growth rates for clams living in sand-filled as opposed to mud-filled boxes within a site, yet for a given sediment treatment, growth rates in their silty environment were actually higher than those in the sandier environment. This suggests that both bottom sediment type and depositional regime are important. Rhoads & Young (1970) found no differences in growth between clams suspended above the bottom turbid layer at a muddy site and those at their "control" (sandy) site, but as mentioned earlier, higher growth rates observed in trays of clams sufficiently elevated above the muddy bottom (versus of those placed within the bottom turbid layer) may have simply reflected higher horizontal food supply due to higher current speeds above the bottom (Dayton & Oliver, 1980). Peterson et al. (1984) observed higher growth rates of clams inside versus outside seagrass beds, and the experimental field study of Irlandi & Peterson (1991) confirmed this observation. In addition, when seagrass was clipped at the base, clam growth and survivorship was higher in intact than in clipped beds (Irlandi & Peterson, 1991). They attributed their results either to predation (seagrass as a refuge), hydrodynamics (seagrass as a baffle to enhance vertical flux of food), sediment stability (seagrass beds as sediment stabilizers in the sense of reducing resuspension), or epiphytic algae (which is higher in seagrass beds). Of these, there is probably more support for the hydrodynamic baffling hypothesis, particularly given that food capture by Mercenaria has been shown to increase with increasing suspended food concentration (Walne, 1972).

All of these studies, taken together, indicate that growth of adult Mercenaria is

not necessarily higher in sandy sediments. In fact, the seagrass studies suggest higher growth rates in relative depositional sites which usually have a substantial silt fraction in the sediment. The studies have not rigorously separated, however, the importance of sediment type versus flow regime.

One explanation for inconsistencies in growth rates across sediment types may be variations in the flux of organic matter (as food) contained within the suspended material. Greater differences in growth rates of Mercenaria have been observed when comparisons were made between different flow environments, as opposed to comparing different sediment treatments, and growth rates were positively correlated with horizontal flux of particulate organic matter, bottom current speed, and suspended chlorophyll concentration (Grizzle & Morin, 1989). This corroborates results of other field (Haskin, 1952; Greene, 1979) and laboratory (Hadley & Manzi, 1984, Manzi et al., 1986) studies showing that Mercenaria growth is positively related to current speed, particularly when suspended food concentration was held constant (Grizzle et al., 1992). These results support the hypothesis that food supply (horizontal flux of suspended organic material) is an important causative factor determining Mercenaria distributions. In the study of Irlandi & Peterson (1991), for example, a strong leading-edge effect (higher growth in upstream animals) was observed in a seagrass bed with asymmetrical tidal flow, suggesting both that food was limiting within the seagrass bed and that within this depositional locale, horizontal food flux determined individual growth rates. A study that directly manipulated near-bed currents in the field, however, showed no difference in Mercenaria growth rates over the range of currents produced (Judge et al.,

1992). Even though food depletion evidently did not occur over these Mercenaria beds, such that increased horizontal food flux resulted in no added benefit, this is not necessarily inconsistent with the hypothesis that advection-diffusion processes that control suspended food concentration can limit the distribution of this and other benthic suspension feeders (e.g., Fréchette et al., 1989).

We propose that sediment type alone is actually a poor predictor of Mercenaria distributions and suspended food supply seems a more likely causative factor. Sediment type may, in some cases, be a correlate of food supply to suspension feeders in that sandy sediments will, on average, be sites of higher advective fluid flux, but the dynamics of food supply to suspension feeders is not as simple as apparently envisioned by Sanders (1958). It is a function of both vertical mixing and advective processes, as well as of upstream food concentration and feeding rates of the animals (e.g., Fréchette et al., 1989; Shimeta & Jumars, 1991). Furthermore, in reviewing the literature on the distribution of Mercenaria populations relative to sediment type, we found no support for the contention that this species is restricted to relatively coarse sediments. Adult abundances are known to be higher in fine sediments containing some coarse (> 2 mm) material such as sand (Walker & Tenore, 1984b) or shells and gravel (Pratt, 1953; Wells, 1957; Carriker, 1961; Walker & Tenore, 1984b), and densities in relatively pure sand may be comparable to those in relatively pure mud (Pratt, 1953). In fact, Grizzle & Lutz (1989) collected Mercenaria off the New Jersey coast from a variety of sediment types ranging from sand to mud, although they provided no density estimates. High population abundances have also been reported in relatively high-flow regions, such as

in the vicinity of outlets to salt-water ponds (Wells, 1957; Carriker, 1959; Mitchell, 1974). Furthermore, although mature individuals of Mercenaria may be found in sandflats (e.g., Peterson et al., 1984), they were more abundant in an adjacent seagrass bed consisting of silty-sands (Peterson et al., 1984; Peterson, 1986; Irlandi & Peterson, 1991).

In summary, neither Sanders' (1958) generalisations on animal-sediment relationships nor Rhoads & Young's (1970) trophic-group amensalism hypothesis appear to be supported by existing data on the distribution and ecology of Mercenaria mercenaria, even though the obligate suspension-feeding mode and short siphon of this species make it an ideal candidate for the proposed amensalistic relationship. Existing data indicate that the distribution of this species is not distinctly associated with a particular sediment type, and there is neither consistent evidence that larvae actively select sandy over muddy sediments, nor that growth and survival of recruits are higher in sandy sediments. There are, however, many studies suggesting that Mercenaria distributions may be related directly to the suspended particulate and near-bed flow regimes above a given sediment. Clearly, relatively high suspended particulate concentrations and relatively high flow speeds are advantageous in terms of food flux to suspension feeders, but the issues of seston quality and the physiological limits to the performance of the filtering apparatus must also be considered, in addition, of course, to biological interactions with other species (e.g., review of Arnold, 1984; Hunt et al., 1987). Understanding the distribution of this commercially important and widely distributed species has suffered from the lack of rigorous predictive theory (see review

of Fréchette et al., in press). This should improve with, for example, the recent development of hydrodynamic models of food supply to suspension feeders (e.g., Fréchette et al., 1989; Monismith et al., 1990; Cloern, 1991; O'Riordan et al., in press) together with experiments that test directly model predictions (e.g., Cole et al., 1992; Butman et al., submitted) and thus reveal other important biological determinants of suspension-feeder distributions.

## OWENIA FUSIFORMIS

Owenia fusiformis (hereafter called Owenia) is a tube-building polychaete that commonly occurs in fine and muddy sand (Fager, 1964; Shimek, 1983; Dauvin & Gillet, 1991). Although predation has been proposed as an important structuring mechanism for Owenia populations (Fager, 1964; Shimek, 1983; Dauvin & Gillet, 1991), there does not appear to be evidence that this results in higher densities of this species in certain sediments (i.e., we are unaware of evidence that Owenia's predators are restricted in terms of sediment type). Owenia is known to occur in very dense assemblages that tend to "stabilise" sediments (i.e., in the sense of decreasing their susceptibility to erosion) (Fager, 1964). Although not explicitly stated by Fager (1964), the presumption seemed to be that the worm-tube assemblage hydrodynamically stabilised the bed via "skimming" flow (i.e., where the top of the tube bed acts essentially as a solid surface in the flow, a new boundary layer develops along this surface, and thus, there is limited exchange of fluid within the worm-tube bed and the overlying water). Subsequent laboratory flume studies have indicated, however, that sediment stability could not have

occurred via this mechanism for Owenia tube densities observed in the field (Eckman, 1981), and that enhanced sediment stability in dense beds of Owenia probably occurs through sediment binding by micro-organisms (Eckman, 1985).

Larvae of Owenia are planktotrophic, and will metamorphose quickly in the presence of fine sand (Wilson, 1932). Although fine sand appears to be the best inducer of metamorphosis, some individuals will metamorphose in response to mud or will metamorphose spontaneously in the absence of sediment (Wilson, 1932). Settlement behaviour in flow has not been evaluated, but recently settled individuals in nature have been recorded in sediments ranging from coarse sand to mud, and their occurrence on the bottom may be a function of water-column transport (Thiébaut et al., 1992). Although active vertical migration by larvae may aid in their retention within a suitable area (Thiébaut et al., 1992), Fager (1964) suggested that dense beds of Owenia may develop in the shallow subtidal from passive accumulation of larvae in sediments located at the heads of rip currents. Larvae can and do settle in high densities in muddy sediments (Yingst, 1978; Dauvin & Gillet, 1991); however, higher post-settlement mortality may occur in mud compared with adjacent muddy-sand (Dauvin & Gillet, 1991). Nonetheless, patches of Owenia may persist in a variety of sediment habitats (Dauvin & Gillet, 1991). Thus, larval selectivity does not appear to account for occurrence of Owenia in fine and muddy sand and we are unaware of fine-scale measurements demonstrating differences in larval availability above adjacent sand and mud habitats.

Feeding in Owenia may range from surface deposit feeding to filter feeding

depending on flow conditions (Dales, 1957). Given the plasticity in feeding mode, there is no clear expectation of distribution pattern based on trophic-group amensalism, although the ability to deposit feed renders unlikely amensalistic exclusion from muddy habitats. Dauvin & Gillet (1991) suggested that Owenia could not occur in substrata where there was not a significant fine-sediment fraction. Growth rates of Owenia individuals in muddy sediments are comparable to those in muddy sand (Dauvin & Gillet, 1991), yet there is higher mortality in pure muds. This suggests that amensalistic interactions cannot explain the distribution of this species, and it is likewise difficult to imagine how a facultative deposit feeder that may stabilise bottom sediments can fit into the trophic-group amensalism paradigm. Feeding plasticity also clearly does not fit into Sanders' (1958) animal-sediment dichotomy.

We do not mean to suggest that the interplay between feeding mode and particle flux does not influence distributions of this and other infaunal species, but that existing paradigms based on functional groups are unsuitable for the complex feeding behaviours that are emerging as infaunal species become better studied under realistic flow conditions. The higher mortality that has been reported for Owenia in mud may reflect post-settlement processes (Dauvin & Gillet, 1991), such as predation, but again this fails to explain why predators might be limited to this (muddy) environment, and why Owenia appears to be somewhat sediment-specific in its distribution. In fact, dense tube mats of this species may result from hydrodynamic concentration mechanisms operating at the time larvae are competent to settle, much as Fager (1964) originally envisioned. The probability of survival of a passively deposited, dense aggregation of Owenia would

depend on both food supply and predators within the depositional locale. The dense tube mat may serve to enhance the food value of sediment within the mat via enhanced microbial activity (Eckman, 1985). Rigorous tests of such scenarios are now technologically possible in large laboratory flumes and could, likewise, be done through field experiments.

## PHYSICAL AND BIOLOGICAL PROCESSES THAT DETERMINE THE SEDIMENTARY ENVIRONMENT

The boundary-layer flow and sediment-transport regime play a critical role in a variety of benthic ecological processes; after a decade or so of rigorous experimentation both in the field and in laboratory flumes, this is now an established fact. Although previous reviews of animal-sediment relationships (i.e., Purdy, 1964; Gray 1974, 1981; Rhoads, 1974; Pèrés, 1982; Probert, 1984) and the studies on which they were based, often acknowledged interactions between sediment type and flow regime, they could not adequately incorporate considerations of the dynamic nature of bottom sediments and the associated near-bed flow regime that have evolved in the last decade.

Very general descriptions of the basic features of hydrodynamic and sediment-transport processes within the bottom boundary layer, particularly with respect to potential effects on benthic organisms, can be found in Nowell & Jumars (1984), Muschenheim et al. (1986) and C.A. Butman (1987). More-rigorous descriptions of bottom boundary-layer flows in the ocean can be found in Wimbush (1976), Komar

(1976a), Madsen (1976), Nowell (1983), and Grant & Madsen (1986), and of sediment-transport processes on continental shelves in McCave (1972), Sternberg (1972, 1984), Smith & Hopkins (1972), Komar (1976b), Drake (1976), Smith (1977), Nowell (1983), B. Butman (1987b) and Cacchione & Drake (1990). In this section we briefly discuss results of recent boundary-layer flow and sediment-transport research that have changed the way in which the sedimentary environment is viewed, and assume that the reader is familiar with the concept of boundary-layer flows. Although some repetition is inevitable, we tailor this discussion to be complementary to those of Nowell (1983), Jumars & Nowell (1984a, b), Nowell & Jumars (1984), and Miller & Sternberg (1988). The purpose of this section is to summarise for benthic ecologists recent conceptualizations of the physical regime in soft-sediment habitats, as well as identifying processes that are still poorly understood.

Surficial sediment distributions are determined by 1) the sediment source (relict or modern), 2) interactions between sediment particles (including adsorption of chemicals), 3) the hydrodynamic regime, and 4) biological effects. All four of these factors can potentially determine whether sediment remains in the bed or is transported by the flow. Regardless of sediment type, the sediment mixture within a given locale generally is not static but is in dynamic equilibrium with the average flow conditions at that site. Surface particles, ranging from sand to clay, are constantly being removed (through resuspension or burial) and added (through deposition or regeneration from depth in the bed). In a purely physical sense (i.e., ignoring, for the moment, factors 1, 2, and 4 above), the sediment is a reflection of the near-bed flow regime. It is often

convenient to characterize the boundary-layer flow environment by the boundary shear velocity ($u_*$). This single-parameter descriptor of the boundary-layer flow and turbulent mixing regime is proportional to the square root of the boundary shear stress ($\tau$), the force per unit area on the bottom. Thus, relatively coarse beds occur in regions that, on average, experience high $u_*$'s (where fine sediments are prevented from settling onto the bed) and, likewise, relatively fine sediments occur in regions that, on average, experience low $u_*$'s (where deposition of fine particles can occur). Within a given sediment, however, other factors, such as particle interactions and biology, can significantly modify characteristics of the sediment mixture making the bed more or less susceptible to erosion and transport.

Sediment transport can be divided into two steps, the first of which involves overcoming particle inertia such that the particle begins to move (called "initiation of motion"); the second step is actual transport. Heavy particles, such as coarse sand grains, begin to roll, hop or saltate along the bottom as "bedload" transport once the shear velocity exceeds that required to initiate motion; this $u_*$ is often referred to as "$u_*$ critical" ($u_{*crit}$). At higher shear velocities, coarse particles make higher and longer excursions into the water column until they remain largely in suspension; the shear velocity at which this occurs is often referred to as "$u_*$ suspended" ($u_{*susp}$). Even at high shear velocities, however, there still is considerable exchange between particles in the water column and on the bed. Very light particles, such as clays, also have thresholds for sediment motion, but $u_{*susp}$ is less than $u_{*crit}$ so once motion is initiated, particles go directly into suspension rather than first moving as bedload. Determining $u_{*crit}$ and $u_{*susp}$

for a given sediment, as well as the hydrodynamic conditions where $u_*$ of the environment exceeds $u_{*crit}$ and $u_{*susp}$, is of great interest to those studying sediment transport. The values of these parameters and the factors that contribute to them are also of paramount interest to benthic ecologists. Indeed, this has been an area of active research in recent years and we summarise briefly the major advances that are relevant to animal-sediment relationships.

Much of the sediment-transport research in the last decade or so has focussed on obtaining more accurate measurements and longer time series of currents very close to the seabed, of sediment and bed characteristics, and of suspended sediment concentrations. Another research focus has been the development of sophisticated models that use these measurements to calculate important sediment-transport parameters, such as $u_*$, $z_o$ (the bottom roughness parameter, which is the effective height above the bed where velocity is zero) and $C_o$ (the reference sediment concentration, which is the sediment concentration at height $z_o$) (e.g., Nowell, 1983; Grant & Madsen, 1986). Considerable progress has been made in developing new instruments that can measure adequately important aspects of the boundary-layer flow (e.g., Williams, 1985; Agrawal & Belting, 1988) and models that use these measurements to calculate parameters such as $u_*$ and $z_o$ (e.g., overview of Cacchione & Drake, 1990), but adequate measurement or model prediction of $C_o$ is still troublesome (e.g., Hill et al., 1988; Drake & Cacchione, 1989; Lyne et al., 1990a, b) and there are ongoing research programs specifically designed to address the issue of adequately measuring and predicting vertical profiles of suspended sediment concentration during transport (e.g., Nowell et al., 1987).

## INITIATION OF SEDIMENT MOTION

The bulk of information on initiation of sediment motion comes from empirical, laboratory studies where $u_{*crit}$ was determined from visual observations of a thin layer of monodispersed sediment. Shields (1936) synthesised observations made on a variety of sediment sizes and types into a single predictive curve, called "Shields curve", which relates two dimensionless quantities composed of fluid, flow, and sediment variables. Miller et al. (1977) updated this curve for measurements made since Shields (1936), but they used only those measurements taken under a restricted set of meaningful laboratory conditions, and this considerably reduced scatter in the data. Thus, for a given size and specific gravity of the sediment, and a given fluid viscosity, $u_{*crit}$ can be determined from Miller et al.'s (1977) modified Shields curve, although some iteration is involved because $u_*$ appears in both dimensionless parameters. Miller et al. (1977) also presented simplified curves that, for example, hold particle density and fluid characteristics constant. Numerous other investigators have constructed similar curves that vary primarily in the range of application and the parameters used to plot the data (e.g., see review in Nowell et al., 1981). Each curve is also constrained in applicability by limitations of the methods, which are often severe in terms of relevance to marine sediments (Miller et al., 1977; Nowell et al., 1981). That is, measurements were made primarily on single size classes of particles distributed in a thin layer, or even a monolayer, on the observation surface, and most measurements have been made on relatively large (e.g., coarse silt and sands), abiotic, non-cohesive particles. Results for

muddy, cohesive sediments are much more complex (e.g., Mantz, 1977; Dade & Nowell, 1991; Dade et al., 1992), and biologically reworked sediments yield widely varying results, as reviewed in Nowell et al. (1981).

Laboratory flume studies on effects of individual benthic organisms (Nowell et al., 1991), groups of individuals of the same species (Rhoads & Boyer, 1982), and cores of sediment containing natural macrofaunal (Rhoads et al., 1978b; Luckenbach, 1986; Grant et al., 1982;) and meiofaunal (Palmer & Gust, 1985; Palmer, 1988b) communities indicate substantial biological effects on sediment transport. Similarly, diatom films (Grant et al., 1986a), mats of purple sulphur bacteria (Grant & Gust, 1987) and exopolymer adhesion (Dade et al., 1990) can significantly affect the entrainment of sand. Studies of individual or species-specific effects versus whole-community effects have their strengths and weaknesses (e.g., see discussion in Nowell & Jumars, 1987). Studies of individuals or monospecific groups of individuals, for example, provide direct information on cause and effect, but are limited in applicability because it is the net effect of all relevant members of the community that determines when sediments are transported in the field. Yet, assessing effects of the "whole community" may be misleading because surface sediments may be disturbed during transport to the lab, and all individuals may not behave naturally (or even survive) in the artificial flume setting. At the least, however, the above-cited studies indicate that benthic biological processes can both significantly increase or decrease $u_{*crit}$ of marine sediments, relative to the abiotic case and, in some instances, the result is non-intuitive (e.g., Nowell et al., 1981).

The state-of-the-art in establishing initiation of motion of natural marine

sediments is germane to this discussion of animal-sediment relationships because, 1) the condition where $u_*$ exceeds $u_{*crit}$ is one useful way to define objectively sediment "stability" (e.g., Grant et al., 1982), which has been touted as a determining factor in the distribution of trophic groups (e.g., Rhoads, 1974), and 2) animals (as well as plants and microbes) can both respond to and directly affect sediments and sediment transport. Moreover, because these effects can vary both temporally (e.g., Rhoads et al., 1978b; Grant et al., 1982; Rhoads & Boyer, 1982) and spatially (e.g., Nowell et al., 1981), relationships between animals and the sediments in which they reside may be very complicated indeed. Unfortunately, the development of a universally predictive relationship (or set of relationships), such as Shields curve, for biologically altered sediments is still in its infancy. This subject should receive considerable attention in the future because field observations of sediment transport cannot be predicted using the theoretical and empirical relationships developed for abiotic sediments alone, and discrepancies may be resolved by inclusion of benthic biological effects (e.g., Drake & Cacchione, 1985, 1989; B. Butman, 1987b; Lyne et al., 1990a, b).

## BEDLOAD VERSUS SUSPENDED-LOAD TRANSPORT

Once in motion, whether particles move as bedload versus suspended load can be roughly determined by the dimensionless ratio $w/\kappa u_*$, where w is the gravitational sinking velocity of the particle and $\kappa$ is von Karman's constant of about 0.4. This ratio is sometimes referred to as the Rouss parameter and represents the relative magnitude of the tendency for particles to fall due to gravity, to the tendency for particles to

remain in suspension due to turbulent mixing. It is the exponent of the solution for the equilibrium suspended-sediment concentration profile and describes the rate of change of sediment concentration with respect to distance above the bed (e.g., Komar, 1986b). Small values of the Rouss parameter indicate that upward mixing of sediment predominates over sinking so that vertical profiles of suspended sediment concentration are relatively uniform, whereas large values of the Rouss parameter indicate that sinking predominates such that sediment is concentrated close to the bed. A Rouss parameter of about one is often used as roughly the division between bedload versus suspended-load transport (e.g., Smith & Hopkins (1972) suggested a value of 0.8) and $u_{*susp}$ for a given particle can be calculated in this manner. The cut-off between bedload and suspended-load transport is operational, however, because the Rouss parameter simply specifies the shape of the equilibrium profile. Concentration profiles for Rouss parameters of 2 to 4 (within the range of so-called bedload transport), for example, show high concentrations of material very close to the bed, but considerable concentrations of particles also occur within the lower 20-30% of the water column (e.g., Komar, 1976b). As mentioned earlier, in reality, there is a lot of exchange between particles in the water column and on the seabed under most flow conditions, but the particles make higher and longer excursions above the bed as $w/\kappa u_*$ decreases.

One of the major problems in predicting suspended sediment concentration profiles is specifying the lower boundary condition, the reference concentration $C_o$. The reference concentration has been theoretically related to the excess shear stress in the bed, $(\tau_b-\tau_c)/\tau_c$, where $\tau_b$ is the stress on the bed and $\tau_c$ is the critical stress of initiation

of motion, by a proportionality constant, $\gamma_o$. Field estimates of $\gamma_o$ have varied over four orders of magnitude (e.g., see compilation in Hill et al., 1988), however, an upsetting result for a so-called constant! Flume experiments by Hill et al. (1988) specified $\gamma_o$, with 95% confidence limits that spanned only about a factor of six. Flume runs were made with but one sediment type, however -- silica sand with a median grain size of 168 μm. Hill et al. (1988) concluded that the physical theory is sound and that the variability in field estimates has resulted from measurement error and improper treatment of one of the critical terms in the calculation.

In fact, measuring suspended sediment concentrations very close to the seabed is problematic because traditional, direct-sampling methods (e.g., pumps) cannot be used within centimetres of the seabed without significantly disturbing the bottom. Indirect measurement techniques, such as transmissometers and optical backscatter sensors can be mounted within 10's of centimetres of the bed, but their sensitivity to particle characteristics requires calibrations using material in suspension at the site to calculate accurately concentration from beam attenuation or backscatter (e.g. Baker & Lavelle, 1984; Moody et al., 1987; Butman & Wheatcroft, 1991, submitted). New measurement techniques involving laser beams or acoustics, for example, that can be mounted a distance from the sediment surface but that make measurements very close to the bottom, are currently being developed and tested for this purpose (e.g., Nowell et al., 1987; Agrawal & Pottsmith, 1991; Lynch et al., 1991).

The suspended sediment concentration profile is relevant to this discussion of animal-sediment relationships because it, together with vertical profiles of velocity,

determine sediment transport rates and directions, and thus also the horizontal flux of food and larvae. These transport rates and directions also provide an objective means of classifying habitats in terms of advective-diffusive flux. Furthermore, it is not just the total flux of material in suspension that may be relevant to animals living in the seabed, but the distribution of this material as a function of height above the bottom (e.g., Muschenheim, 1987b; Fréchette et al., 1989). Sediment moving as bedload versus suspended load, for example, may be an important factor determining animal distributions (see next section). Moreover, like initiation of sediment motion, benthic organisms can directly affect suspended sediment concentration profiles, for example, by pelletizing the bed and changing the transport characteristics of the particles (e.g., Taghon et al., 1984; Komar & Taghon, 1985), by directly ejecting particles into suspension (e.g., Rhoads, 1963), and by grading the sediment bed through their feeding activities such that surficial sediments differ from the sediment mixture deposited originally (e.g., Rhoads, 1967; Jumars & Wheatcroft, 1989; Wheatcroft, 1991a, 1992; Butman & Wheatcroft, submitted).

## THE BOUNDARY-LAYER FLOW REGIME

The development of increasingly more sophisticated instruments for making detailed measurements of the boundary-layer flow environment (e.g., Butman & Folger, 1979; Cacchione & Drake, 1979; Downing et al., 1981; Williams, 1985; Agrawal & Belting, 1988; Agrawal & Pottsmith, 1991; Lynch et al., 1991) and of refined, coupled, boundary-layer flow and sediment-transport models (e.g., Smith, 1977; Smith &

McLean, 1977; Wiberg & Smith, 1983, 1989; Grant & Madsen, 1979, 1982; Trowbridge & Madsen, 1984a, b; Gross, 1986; Glenn & Grant, 1987; Gross & Dade, 1991) has considerably advanced our understanding of interactions between the boundary-layer flow and sediment-transport regimes. What is needed, however, are more extensive field tests of the models, especially in muddy environments where biological processes may be important, and subsequent refinement of the models based on these results (e.g., Nowell & Hollister, 1985; Nowell et al., 1985; Nowell et al., 1987).

One of the major advances in this field has been an enhanced appreciation of the role of waves and wave-current interaction in the structure of the boundary-layer flow and sediment transport. It is now well accepted, for example, that the bottom stresses generated simultaneously by waves and steady currents are not simply additive; the steady current experiences what amounts to an enhanced, "apparent" bottom roughness due to the waves and this must be accounted for in calculations of the total bottom stress (Smith, 1977; Grant & Madsen, 1979). Likewise, the relatively new concept that wave-generated boundary shear stress is a more effective means of resuspending bottom sediments than the stress generated by steady currents has now reached fruition (e.g., Grant & Madsen, 1986; Cacchione & Drake, 1990). This means that in regions with significant wave activity, in addition to traditional measurements of the "steady" currents, adequate characterization of the boundary-layer flow and sediment-transport regimes requires measurements of currents within the wave boundary layer (of order centimetres thick) and of the wave field (e.g., Grant & Madsen, 1986).

In addition to heightened awareness of the importance of waves, there is growing

appreciation for the potential of benthic organisms to affect the structure of the boundary-layer flow both directly, through their effects on seabed roughness (e.g., Nowell et al., 1981; Nowell, 1983; Cacchione et al., 1983; Wheatcroft, 1991b), and indirectly, through their effects on the stability (defined here as the susceptibility of sediment to transport) of the seabed (e.g., Eckman, 1981, 1985; Nowell et al., 1981; Grant et al., 1982; Luckenbach, 1986). Seabed stability can affect the structure of near-bed velocity profiles in that sediment transporting as bedload or in suspension dissipates energy in the flow, resulting in an enhanced, apparent bottom roughness (e.g., Grant & Madsen, 1982; Glenn & Grant, 1987; Wiberg & Smith, 1989).

We stated earlier that sediments at any given locale roughly reflect the "average" near-bed flow regime, but this really applies only to long-term averages and, even so, it is an over-simplification. In fact, physical processes operating at different time and space scales transport sediments in differing amounts and directions, sometimes resulting in dramatic temporal changes in the nature of the bottom sediments at a given site. From long time-series measurements of the flow and sediment-transport environment on Georges Bank, Massachusetts, for example, B. Butman (1987b) identified at least four physical processes responsible for sediment movement: tides, storms, internal waves, and warm-core Gulf Stream rings. Each of these processes operates at different time and space scales and the processes may occur simultaneously or separately. The amount of sediment transported, as well as the frequency and direction of transport, also vary as a function of the physical forcing. In fact, the amount of sediment transported daily, due to tidal-driven flows, for example, compared to episodic transport due to storms, is

an important unresolved issue in sediment transport today (e.g., Cacchione & Drake, 1990; Lyne et al., 1990).

Likewise, whether or not benthic biology can significantly affect flows and sediment transport depends, in part, on timing. Biological effects on seafloor stability may be more pronounced, for example, during the autumn on the northeast coast of the United States, when animals are abundant (i.e., following successful recruitment) and the water is relatively warm so that metabolic rates are high. As the season progresses, reworking activities of the animals tend to decrease as water temperature drops and this, coupled with increased storm activity, can result in reduced biological binding of sediments, making them more susceptible to erosion. This sequence has been observed, for example, on Georges Bank from bottom photographs taken by cameras mounted on tripods (B. Butman, 1987a) and in Buzzards Bay from direct sampling of the seabed (Grant & Butman, 1987; C.A. Butman and C.M. Fuller, unpubl. obs.).

These results underscore the potentially complex nature of both the flow and sediment-transport regime, and how they influence animal-sediment relationships. The physical regime must be evaluated in view of the spatial and temporal scale of interest. In most cases, for example, using a single current meter mounted near the water surface is probably inadequate to characterize the "flow environment" of the benthos, particularly where waves are important (e.g., Miller & Sternberg, 1988). And, once again, it is clear that benthic organisms can both affect and be affected by boundary-layer flows.

# DIRECT CORRELATES OF SEDIMENT TYPE THAT MAY DETERMINE INFAUNAL DISTRIBUTIONS

Given that the bottom sediment, for the most part, reflects the boundary-layer flow and sediment-transport regime, correlations between animal and sediment distributions may be caused not by any particular aspect of the sediment itself, but by the physical processes that created that particular sediment environment. We discuss such possibilities under the separate headings of "hydrodynamic regime" and "sediment-transport regime", but of course these regimes are related and may also operate in concert as causal factors in species distributions.

In this and the next section, potential effects of the flow and sediment-transport regime on species distributions are proposed as structuring factors, in addition to those discussed earlier. We are not touting hydrodynamics and sediment-transport processes as the only or even the major structuring agents of infaunal species distributions to the exclusion of other processes. We are, instead, seeking to obtain a more comprehensive view of benthic biological processes within the context of their physical environment.

## HYDRODYNAMIC REGIME

The boundary-layer flow regime may affect directly animal distributions through drag and lift forces on above-ground structures, such as tubes, or on the animals themselves. The drag on a structure in turbulent flow is proportional to the frontal surface area (i.e., relative to the flow direction) of the structure and velocity squared, such that relatively

small increases in velocity result in much larger increases in drag. Although the size, shape, and stiffness of tubes and appendages of benthic organisms, for example, are likely to have evolved to withstand drag forces in the environment, there may be structural or biological limits to tube and appendage stiffness and morphology, and animal distributions may reflect these limits. That is, there may be an upper limit to flows in which tube dwellers can reside, due to the drag on feeding appendages, as well as on tubes. To our knowledge, this possibility has not been explored for infaunal organisms, but the studies of Koehl (1977a, b, c), for example, on the distribution of sea anemones relative to the flow forces they encounter suggests that animal distributions can, in fact, be determined, at least in part, by the fluid dynamic environment (see also Koehl, 1984). Lift forces are likewise a function of velocity squared and may determine animal distributions, as suggested by O'Neill (1978) for sand dollars.

Passive, suspension-feeding, tube-dwellers are also known to utilize the flow regime to enhance food capture. (The broader subject of food supply to suspension feeders as a function of boundary layer flow is discussed later.) In a steady flume flow, Carey (1983) showed that tubes of the terebellid polychaete Lanice conchilega, which project above the sediment surface, create a characteristic vortex pattern downstream. The upward motion associated with the vortices may increase particle resuspension in the lee of the tube, particles that may then be captured as food by the tentacular crown of the worm. Likewise, Johnson (1990) suggested that the spacing of individuals within a bed of phoronids enhances the incorporation of benthic food items into their diets through passive entrainment by the flow. In addition, some tube-dwellers are known

to orient tube openings relative to flow direction (e.g., Brenchley & Tidball, 1980; Vincent et al., 1988), a strategy that may decrease the energy required for particle capture.

Very dense assemblages of tube dwellers potentially can enhance particle retention time within the tube bed via skimming flow (described earlier), although it is unclear if natural populations of many species occur in sufficient densities for this to occur (Eckman, 1981). The flow regime associated with tubes protruding above the bed may indirectly result in a stabilised sediment bed (in the sense of decreasing the probability of sediment erosion) via enhanced nutrient flux to and thus microbial growth within the sediments (Eckman, 1985). The stabler bed may then facilitate the existence of species that otherwise could not occur within that flow and sediment-transport regime.

The irrigation of pore waters, and thus, the depth within the sediment that is oxygenated is controlled by the near-bed flow regime and pore spaces (which correlate with sediment size). Depth distributions within the bed of infaunal organisms that are sensitive to anoxia may thus be determined by the boundary-layer flow. In Buzzards Bay, Massachusetts, for example, the depth distribution within the sediment of the head-down, deposit-feeding polychaete Mediomastus ambiseta varies temporally -- worms reside closer to the sediment surface in the warm summer months than during winter, apparently because of the very shallow redox layer in the summer (C.A. Butman and C.M. Fuller, unpubl. obs.). Other aspects of pore-water chemistry (e.g., sulphide concentrations) may similarly be controlled by the near-bed flow regime (e.g., Ray & Aller, 1985) and limit species distributions.

For small, near-surface-dwelling organisms that are susceptible to erosion, such as some meiofauna species (larval supply is treated elsewhere), the organisms may be transported directly by the near-bed flow regime. Palmer & Gust (1985; see also Bell & Sherman, 1980) have shown, for example, that meiofauna can be resuspended and transported by everyday tidal flows on intertidal mudflats. There appears to be a behaviour basis for meiofauna taxa that are susceptible to passive transport (Palmer, 1984). Depth distributions of meiofauna within the sediment bed are also known to be both taxon-specific and a function of flow regime (Palmer & Molloy, 1986; Fegley, 1987). The broader topic of marine meiofaunal distributions as a function of the boundary-layer flow regime has been reviewed recently by Palmer (1988a).

The hydrodynamic regime also may be utilised by animals to enhance the probability of fertilization during spawning, or to otherwise facilitate gamete dispersal. Barry (1989) has shown that a reef-building tube-worm spawns in response to big storms, evidently to enhance gamete dispersal. Tidally-timed spawning behaviour has also been demonstrated for several invertebrate species (e.g., Stanczyk & Feller, 1986).

## SEDIMENT-TRANSPORT REGIME

Direct effects of the near-bed flow regime on infaunal species distributions may not be nearly as profound as direct effects of the sediment-transport regime, which reflect both the flow and suspended-sediment concentration profiles above the bed. Not only can the sediment-transport regime determine directly the food supply to suspension feeders, and indirectly to deposit feeders (i.e., through deposition and incorporation of organic

material within the bed), but it also reflects the "stability" of the sediments. It is this latter point that will be discussed here; issues of food supply will be discussed in the next section.

Viewing the sediment environment in terms of the overlying sediment-transport regime, in addition to the propensity of the sediment to remain in the bed, may provide more direct insight into the ways in which sediment transport processes might effect or affect infaunal distributions. We are not implying that the classical issues of tube building and mobility, for example, as a function of sediment stability (e.g., Rhoads, 1974) are not relevant to species distributions; we are merely suggesting that the sediment-transport regime above the sediment-water interface should be considered at the same time. We will not review again here ideas on potential sediment-transport effects on infaunal organisms, as discussed by Jumars & Nowell (1984a,b) and Miller et al. (1984). Instead we suggest criteria by which sediments may be classified as "stable" or "unstable" that include information on the sediment-transport regime.

As discussed earlier, classification of sedimentary habitats in terms of sediment stability has not been rigorous in the past because of the lack of a physically meaningful and objective criterion for "stability". Based on our earlier discussion of the contemporary view of physical processes within the bottom boundary layer, we suggest two ways that sediment stability may be defined objectively. First, the average $u_{*crit}$ (and $u_{*susp}$) for a given sediment could be used to classify natural sediment beds in terms of their susceptibility to erosion (and transport), relative to the abiotic case, as was done in Grant et al. (1982). This kind of classification may be much easier for some

sediment types than others. For example, muddy sediments may be problematic because there can be a surficial "fluff" layer of light, flocculent material that is so easy to erode that it virtually remains just barely suspended above the bottom in most flows (e.g., Stolzenbach et al., 1992), but the underlying, bioturbated mud may be tightly bound by mucous secretions such that it is much more difficult to erode than abiotic, muddy sediment. Even given such difficulties, defining sediment stability based on an objective criterion such as $u_{*crit}$ would avoid the terminological ambiguity that presently exists in the literature (see also Jumars & Nowell, 1984a).

Second, sediment stability could be defined in terms of actual, average, vertical profiles of suspended sediment concentration and sediment flux. This would indicate that amount of material actually transported as suspended load versus bedload, which may be much more meaningful to the ecology of infaunal organisms. In practice, the field measurements required for this kind of classification may be difficult, but not impossible, particularly given the new technological developments for measuring suspended sediment concentration and velocity profiles, discussed earlier.

## INDIRECT CORRELATES OF SEDIMENT TYPE THAT MAY DETERMINE INFAUNAL DISTRIBUTIONS

Two potentially important structuring variables of soft-sediment communities are larval and food supply. Although these variables often strongly correlate with sediment type, they are functionally unrelated and could result in sediment-specific associations

of organisms with sediments where no causality of sediment type and faunal distributions exists.

## LARVAL SUPPLY

The last decade has seen a surge of interest in larval ecology, particularly from the standpoint of how supply may influence spatial pattern (e.g., Lewin, 1986). The recognition of the importance of larval availability is not new (e.g., see Young, 1987), however, and annual fluctuations in larval availability have long been known to contribute to temporal variation in local species pattern (e.g., Thorson, 1957). Nonetheless, the linkage between physical and behavioral aspects of larval dispersal and settlement (e.g., Eckman, 1979, 1983; Hannan, 1984; Butman, 1989) over realistic spatial scales (e.g., C.A. Butman, 1987) is changing our perception of how patterns are initially established. Indeed, the present view of larval dispersal is very different from Petersen's (1913) perception of a "rain of larvae" to the seafloor followed by differential mortality.

Early small-scale, sediment-selection studies conducted in still water (Table II) led to a general acceptance of the notion that habitat specificity in species distributions may be the result of active habitat selection by larvae. These experiments, as well as the scales at which they were conducted, are discussed in detail in C.A. Butman (1987) and will be treated here only briefly. A number of the species tested displayed some form of habitat selectivity in still water (Table II); however, very few choice experiments were conducted in realistic flow regimes, thus making it unclear how

selective behaviour may operate in nature. For at least some soft-sediment species, mean horizontal flow speeds greater than their maximum horizontal swim speeds occur at heights of only several body lengths above the bottom (Butman, 1986). Thus, hydrodynamics is likely to affect larval settlement at least as some spatial scale.

Laboratory flume studies designed to test directly the relative importance of passive deposition versus active selection over scales of centimetres in slow, turbulent flows suggest that both passive and active processes contribute to settlement patterns. In flow and still-water experiments, Capitella sp. I selected a particular sediment type on a fine spatial scale although sediment choice appeared to be hydrodynamically constrained by flow direction (Butman et al., 1988; Butman & Grassle, 1992; Grassle et al., 1992b). Larvae of Mulinia lateralis are also capable of habitat selection in still water and flow (Grassle et al., 1992a); however, selection in flow was more consistent among replicate experiments, suggesting that near-bottom currents may facilitate selection by transporting these relatively poor swimmers across different sediment environments for their perusal. Experiments testing selectivity of Mulinia lateralis and Capitella sp. I transported over small depressions containing different sediment types indicated that larvae were entrained in depressions like passive particles, but were generally able to escape if the substrate was unsuitable (Snelgrove et al., 1993). In general, it appears that these species are delivered to the bed somewhat passively, where they decide actively whether to stay or to leave. The recent flume study of Jonsson et al. (1991) indicated that bivalve pediveliger dispersal may be heavily constrained by near-bottom flows. They suggested that the vertical shear within the viscous sublayer

in hydrodynamically smooth, turbulent flow may result in limited upward swimming by pediveligers, that naturally swim in helices. The shear-induced torque on the larvae could make swimming above the sublayer impossible, thus confining pediveligers to the water immediately (i.e., millimetres) above the sediment. Thus, flume studies suggest that hydrodynamics as well as behaviour, are important, but admittedly relatively few studies have been done and it would be premature to try to draw generalizations based on these studies alone.

One of the few early field studies to consider hydrodynamics within the context of larval transport and settlement was Pratt's (1953) survey of Mercenaria mercenaria distributions in Narragansett Bay. Adult densities were highest in fine sediments with shell and rock, and Pratt suggested that roughness features might provide microhabitats of low velocity suitable for settling in an otherwise high-flow environment, which would be an advantageous feeding environment for the suspension-feeding adults. Enhanced sand dollar settlement has also been noted on cobbled sand compared to a sandflat (Birkeland et al., 1971) with a similar possible explanation. Furthermore, Tyler & Banner (1977) noted a correlation between fine sediment and adult ophiuroid density, and attributed it to hydrodynamic effects on larvae -- larvae might be sorted and deposited similarly to fine sediments in low-energy areas.

Efforts to actually sample larvae in situ on a fine scale have also suggested that hydrodynamics may impose considerable constraints on distribution and eventual settlement site. Fine-scale sampling of larvae in estuaries (see review by Stancyk & Feller, 1986) suggests that distributions are heavily constrained by physical processes.

Meroplankton distributions in Kiel Bay appeared to be tied to the water masses in which they were spawned (Banse, 1986), suggesting that these organisms behaved as passive, neutrally buoyant particles. Similarly, sand dollar larvae on the California coast were found in roughly comparable numbers, but asynchronously, over sand dollar beds and in less suitable habitats (Cameron & Rumrill, 1982), again suggesting passive transport and deposition. Larvae of the polychaete Pectenaria koreni showed vertical stratification in the water column in the western Bay of Seine when turbulence was low, but they were homogeneously distributed when turbulence was high, suggesting passive mixing during high turbulence but possible active migration during low turbulence (Lagadeuc, 1992). A similar effect was observed in Owenia fusiformis larvae (Thiébaut et al., 1992); however, only early stages were vulnerable to passive mixing and the resulting seaward transport. Older stages were able to migrate to strata where they were retained in the bay. Tidal transport of larvae may also be an important dispersal mechanism. Levin (1986) found ten-fold variations in larval abundance in Mission Bay, California, and suggested that a large patch of larvae was oscillating across the mudflat with flood and ebb tides. Unfortunately, extensive time-series measurements of larval distributions over wide spatial scales are relatively rare in non-estuarine habitats. Particularly needed are large scale simultaneous measurements of larval distribution and concurrent measurements of initial larval settlement.

Several studies have observed comparable settlement over adjacent areas with different sediment types (Smidt, 1951; Muus, 1973) or biological structures (Luckenbach, 1984), suggesting that larvae of at least these species were non-selective

or, if they settled passively, that the depositional regime was similar among the different sampling locales at the time of settlement. In one study where differences in newly settled recruits of the bivalves Macoma balthica (Günther, 1991) and Mya arenaria (Günther, 1992) were documented along a sediment gradient, it was not possible to determine whether the pattern was produced by active selection or passive deposition. In none of these studies, however, was variability in larval supply across sediment types measured, although the spatial scale of sampling was generally small.

Experimental field manipulations designed to evaluate the importance of flow and larval distribution have suggested that fine-scale hydrodynamics may be important in larval supply. Eckman (1979) found differential recruitment in intertidal species of tanaid crustaceans and direct-developing polychaetes near simulated animal tubes, suggesting that the distribution of benthic larvae was influenced by fine-scale hydrodynamics. In a later study (Eckman, 1983), tube spacing and density were also shown to influence recruitment, confirming that hydrodynamics can have a very large impact on organism distribution. It is unclear, however, whether the patterns observed reflected passive deposition or active response of larvae to some aspect of the different flow environments or something that correlates with fine-sediment distributions, such as organic carbon. Field experiments by Kern & Taghon (1986) on passive accumulation near epibenthic structures, where an enrichment treatment was also tested, indicated that both active behavioral responses and physical-transport processes determine small-scale recruitment patterns. Similarly, Savidge & Taghon (1988) demonstrated enhanced settlement in depressions compared with flush sediment.

Although their data suggested passive accumulation, active response to elevated organic matter could not be discounted. Utilizing biases in sediment trap collection efficiencies, Butman (1989) showed that traps with higher collection efficiencies for passive particles tended to collect higher numbers of most species of larvae compared to traps with lower passive collection efficiencies, suggesting that larvae may be passively transported and deposited like sediment particles.

Given that flow may determine where larvae are transported, the potential importance of hydrodynamics in distributions of infaunal species becomes obvious. Larvae may be sorted like passive particles, and thus may be weakly associated with a given sediment type for this reason alone. Predicting the onset of larval competency is a critical issue in larval ecology at present (e.g., Bachelet et al., 1992); however, it is known that some species may delay metamorphosis for at least several weeks without any detrimental effect (e.g. Pechenik & Cerulli, 1991) whereas others have a relatively narrow window where selective settlement is possible (Grassle et al., 1992b). Short development times to competency increase the probability of at least staying within the vicinity of the habitat of the adult, which may be favourable. If the competency period is short, this increases the likelihood of settling on an unsuitable substrate, particularly if larvae are vulnerable to passive hydrodynamic deposition. An extended development time in the plankton might, however, increase the likelihood of dispersal away from the parental habitat, perhaps to unfavourable sites (e.g., Jackson & Strathmann, 1981). This is an important subject area for future research.

Flow may also redistribute settled individuals and this may be an important

means of dispersal, particularly for direct developers (e.g., Sigurdsson et al., 1976). Substantial postlarval transport has been noted for a number of species, including Cerastoderma edule (Baggerman, 1953), Mya arenaria (Matthiessen, 1960; Emerson & Grant, 1991), and Macoma balthica (Günther, 1991). Given that fall velocities of competent larvae are within the range of fine silts (Butman et al., 1988a; Grassle et al., 1992b), and post-larvae are within the range of sands (e.g., Peterson, 1986; C.M. Webb & C.A. Butman, unpub. data) passive redistribution of settled individuals is likely to be more common in high-energy environments, and may therefore be important to animal-sediment associations in sandy, erosional areas.

In summary, the hydrodynamic factors that determine the sedimentary composition of an environment may similarly determine the larval supply to that habitat. Although there is experimental support for passive deposition operating at several spatial scales, results are confounded, for the most part, by active selection for organic-rich sites where fine particles accumulate. Thus, larval supply is an indirect correlate of sediment type that could result in what appear to be consistent animal-sediment associations. Sorely needed are field experiments specifically testing the passive deposition hypothesis, including quantification of subsequent survival of recruits within their depositional (or actively selected) locales.

## FOOD SUPPLY

Food supply to benthic organisms is heavily dependent on local flow conditions, which we have shown to be a primary determinant of sediment distributions. Muddy

sediments generally have a higher organic content than sandy sediments because organic matter tends to be more closely associated with the lighter, depositional sediment fraction that accumulates in low-flow areas. Within such flow environments, rates of particle transport tend to be low in the horizontal and high in the vertical. In sandy environments, fine particles may still deposit, but they tend to resuspend quickly and are transported both vertically (upward mixing) and horizontally, resulting in little fine sediment and organic accumulation. Thus, the organic content of sediment is affected by the large-scale flux of particulate matter and differential binding to sediment particles.

Even within a sedimentary regime, hydrodynamics influences sedimentary carbon and thus the infauna. This is perhaps best illustrated by summarizing studies on effects of small-scale topographic variation on the distribution of organic matter and infauna. In a variety of habitats, ranging from shallow water (VanBlaricom, 1982) to the deep sea (Grassle & Morse-Porteous, 1987), organic material has been observed to accumulate in small (tens of centimetres) depressions, as a direct result of their trapping characteristics. Not surprisingly, in different flow environments, coarse (Nelson et al., 1987) or fine sediment (Risk & Craig, 1976) may also accumulate in depressions, although this would not be expected in habitats with homogeneous sediments. Variation in topography and organic content has been related to faunal distributions in a variety of habitats. Intertidal amphipods tend to accumulate in ripple troughs (Sameoto, 1969), which may be an active response of the organisms to enhanced detrital accumulation in troughs; however, in some instances, amphipods (Grant, 1981) and nematodes (Hogue

& Miller, 1981) have been shown to occur in greater abundance in ripple crests than troughs. Organisms may respond actively to elevated organic levels resulting from material accumulating in troughs during low tide, followed by passive burial in the following high tide by migrating ripples. Higher densities of colonizers have been observed in depressions compared to defaunated flat areas (Savidge & Taghon, 1988), and passive advection was postulated as a probable explanation. Diatom films on the surface of sediment may also vary across topographic features. Under calm flow conditions, thicker films may be found in ripple troughs and slopes (Grant et al., 1986a). Such differences in film thickness may be an important source of food variation. Detritus, worm tubes and algae have all been observed to accumulate in pits created by ray foraging (VanBlaricom, 1982), and changes in carbon to nitrogen ratios have suggested that initial detritus was succeeded by bacteria and algae, and then by macrofauna. Although this has the potential to be an important source of heterogeneity in some habitats, walrus feeding pits, for example, have elevated organic content but very modest faunal differences compared to adjacent undisturbed areas (Oliver et al., 1985). Thus, the magnitude and types of "responses" to small-scale variation in organic content, be they active or passive, are almost certainly a function of the ambient faunal composition and the local flow regime.

These studies indicate that fine-scale flow variation may result in a variety of different types of food patches and infaunal responses. Unfortunately, they fail to clarify whether colonizers are passively entrained with the organic matter, which they may then utilize, or whether they are actively responding to it. However, they do

illustrate how the same small-scale hydrodynamics that can influence sedimentary composition may also influence food availability and result in faunal responses (be they active or passive).

The availability of food in suspension may also be limiting to the distribution of many organisms. Because suspension feeders remove organic matter from water passing by them, rates of horizontal and vertical transport may determine which environments they inhabit. However, the process of filter feeding is complex; a variety of different particle-trapping mechanisms may be used (e.g. Rubenstein & Koehl, 1977; LaBarbera, 1984; Shimeta & Jumars, 1991), and the degree and type of "suspension feeding" may range from flow-dependent deposit and filter feeders (e.g. Taghon et al., 1980; Miller et al., in press) to organisms that resuspend depositional material for feeding (e.g. Mills, 1967) to active and passive suspension feeders (Jφrgensen, 1966). Thus, the relationship between suspension feeder distribution and flow regime is extremely complex.

Suspension feeders become proportionally less important with increasing water depth, perhaps as a result of a decrease in flux of organic matter where currents are generally weaker (Sanders et al., 1965; Jørgenson, 1966). Passive suspension feeders may also be confined to flow environments with greater horizontal fluid flux than active suspension feeders, although the dichotomy of feeding type may be better described as a gradient (LaBarbara, 1984). Flume studies have shown that the polychaete Spio setosa filter feeds several centimetres above the bottom, which may be a response to the higher organic seston flux at this height compared to the higher proportion of dense inorganic particles closer to the bed (Muschenheim, 1987b), again suggesting that horizontal flux

is important. It is difficult, however, to imagine a mechanism by which infaunal organisms can detect and respond to a dynamic quantity such as food flux; it seems more likely that the biological response is to a scaler variable, such as suspended food concentration (e.g., Fréchette et al., submitted), although food concentration, flow speed and horizontal flux may be so correlated that ultimately it may not matter precisely which of these variables is "most" responsible.

Although there is a general tendency to think of suspension feeders in terms of horizontal flux and food supply, there is evidence that horizontal flux may not be the only issue. Higher growth rates of Mercenaria mercenaria have been observed in seagrass beds compared to adjacent sandflats (Peterson et al., 1984; Irlandi & Peterson, 1991), despite the lower horizontal food flux through the seagrass. Higher growth may be a result of enhanced total particle flux (i.e., horizontal and vertical) created by the seagrass baffling. We suggest that, in all environments, it is important to consider the three-dimensional nature of fluid and particulate flux because horizontal and vertical flux are not, in fact, separate in nature (e.g., Fréchette et al., 1989).

We have been deliberately brief in discussing food supply because a detailed treatment of the subject is beyond the scope of this review. We have, instead, chosen some specific examples to illustrate that infaunal distributions may, at least in some instances, be influenced by food supply, which is another correlate of hydrodynamics, and thus an indirect correlate of sediment type.

## ANIMAL-SEDIMENT RELATIONSHIPS ON GEORGES BANK, U.S.A.

During the late 1970's and early 1980's, a multidisciplinary study of Georges Bank was undertaken in response to plans to begin petroleum development in an extremely important commercial fishing area. Although the goals of this study were to quantify the potential impact of drilling activity, the physical, geological and biological studies conducted prior to production drilling (which ultimately did not take place) provide a useful data set to illustrate the dynamic nature of sedimentary environment of infauna on continental shelves and to provide examples of the "gestalt" of the sedimentary milieu that was mentioned in the introduction to this paper.

The majority of the Georges Bank area is covered by sand having a relatively low silt content, with the exception of a single area referred to as the "Mud Patch" that represents the only area of the eastern United States outer continental shelf where silt-clay content exceeds 30% (Milliman et al., 1972). The fauna at this site, as well as in adjacent areas were carefully characterized in 1981-1982 (Maciolek & Grassle, 1987; Michael, 1987). The fauna at the Mud Patch was markedly different from that in the samples collected from a number of sandy stations adjacent to its eastern border (Maciolek & Grassle, 1987). Of the ten most abundant species at the Mud Patch, four were not found elsewhere, four were found at only one or two other stations, and two were widely distributed over the sampling area. Only one other station showed a faunal affinity with organisms in the Mud Patch, and although the station was geographically closest to the Mud Patch, the sediment content was almost exclusively sand (Maciolek

& Grassle, 1987). Similarly, Michael (1987) found that four of the six most abundant species were unique to the Mud Patch, one was found only at one other station, and one was widely distributed. Thus, these results are consistent with those of most studies on animal-sediment relationships that we have reviewed here; some species are unique in their distributions, others show some overlap with other habitats, and some are very widespread (e.g., Table I).

In addition to a large difference in silt-clay content, the Mud Patch has a substantially higher organic carbon content than adjacent sandy areas (8-11 mg/g and approximately 0.5-3.5 mg/g accordingly; Michael, 1987). This can be attributed to sediment-transport processes within the area (Figs. 1 and 2). Prevailing currents carry sediment largely to the west, where they weaken and dump fine sediments in the Mud Patch (e.g., Bothner et al., 1987). The transport of fine sediments into the Mud Patch from sandy areas to the east is a result of very different hydrodynamic conditions in the areas (B. Butman, 1987b). To compare the hydrodynamics at the Mud Patch to those in the sandy habitats, we have selected data from Mud Patch station 49 (Fig. 1), and sandy station 11 (Fig. 2). Flow speeds at 1 m above the bottom are much slower at the Mud Patch (≈12 cm/s, maximum of 35 cm/s) than those in the sandy areas (>20cm/s, maximum of 55 cm/s). Not surprisingly, the boundary shear stress resulting from current and wave movement across the bottom is higher at the sandy site. Although there is more energy to suspend and transport sediment at the sandy site, the amount of suspended sediment is much higher at the Mud Patch. This is because there is virtually no fine sediment that can be resuspended at the sandy site, and these coarse-grained

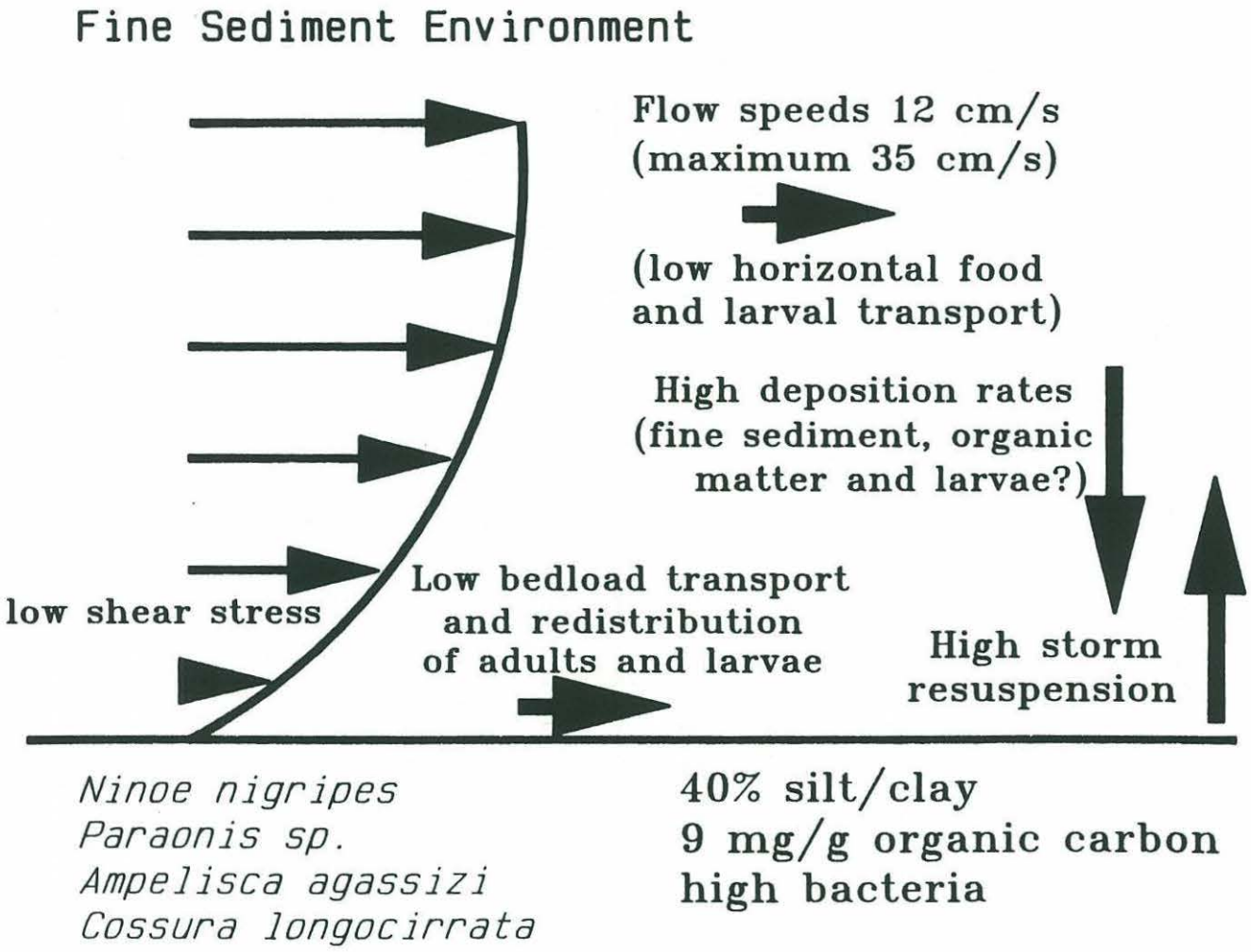


Figure 1. Dominant species at the "Mud Patch" on Georges Bank and physical factors that may influence their distributions (see text for sources)

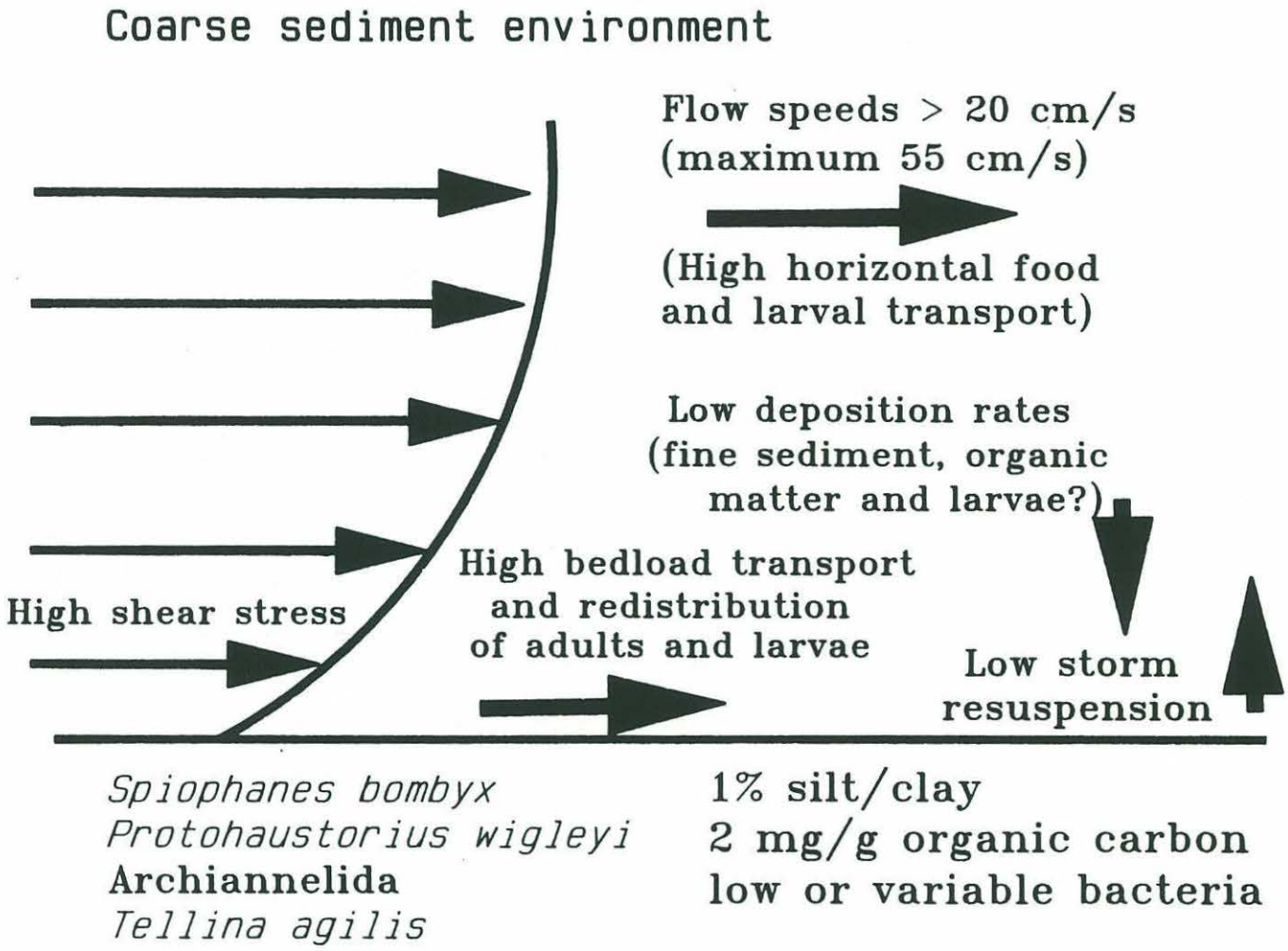


Figure 2. Dominant species at a sandy site on Georges Bank and physical factors that may influence their distributions (see text for sources)

sediments require extremely high flows for suspended-load transport. Sediment transport away from the Mud Patch occurs largely during storm activity (Lyne et al., 1990); at other times, sediment resuspension is much lower and horizontal transport is minimal. Indeed, the presence of the Mud Patch suggests that at least over a geological time scale, more fine sediment has been transported into the Mud Patch than out of it, and a crude budget suggests that at present, transport in and out roughly balance (B. Butman, 1987b). Furthermore, the lack of suspended material at sandy sites does not mean that the sediment is stable. The source of fine sediments for the Muddy Patch is thought to be westward transport of fine material from the sandy areas (B. Butman, 1987b). Though present in only very small amounts, fine sediments are resuspended and quickly transported westward by currents, and fine material is deposited as currents weaken over the Mud Patch. Even larger sediment grains at the sandy site are far from stable. The presence of persistent, wide ripples at the sandy site suggests that bedload transport occurs on a fairly regular basis, as a result of tidal currents and storms (Lyne et al., 1990).

These data do not offer a clear explanation concerning animal-sediment associations at the Mud Patch and adjacent sandy areas, but they do illustrate the complex, dynamic nature of the sedimentary environments. Currents vary dramatically in the two areas, and this results in differences in horizontal and vertical flux of materials (e.g., sediment, food, larvae), supply and fate of these materials between environments (e.g., high horizontal transport of sediment and detritus out of sandy environments and deposition into muddy environments), and the dynamics of materials

within the environment (differences in fate of resuspended material in a muddy habitat compared with a sandy habitat).

## SUGGESTIONS FOR FUTURE RESEARCH

In the process of reviewing the existing literature on the distributions of organisms in marine soft-sediment habitats, a deficiency of data was apparent in several areas. Though a number of studies have looked at species interactions, we were surprised at the paucity of data on the natural history of organisms, particularly under realistic flow conditions. In trying to evaluate sediment-feeding relationships, for example, we found that the feeding ecology within natural flow regimes is known for only a few species, which is understandable given the relative infancy of the field of organism-flow-sediment interactions. Flume studies and video imaging are beginning to change the way we think about trophic groups and feeding strategies, and similar studies on species interactions are bound to be interesting. Likewise, timing and duration of reproduction is largely anecdotal, based on scattered plankton tows or gonad indices. We are unaware of any attempt to track soft-sediment larvae from fertilization to settlement, admittedly an extremely difficult task but one that would be well worth the effort. Similarly, frequent monitoring of larval supply over adjacent, contrasting habitats and evaluating initial settlement (before potential biological interactions take place) relative to recruitment would also help determine the role of hydrodynamics and larval selectivity under natural circumstances. Studies on settlement and colonization

have often suffered from insufficient resolution in temporal sampling, thus introducing a number of potential confounding factors. Finally, because of the complex nature of the sedimentary regime in most soft-sediment habitats, biologists need to begin to measure meaningful sediment and flow parameters for interpreting biological data within the context of the natural, physical environment.

In general, well-defined, unambiguous experiments are sorely needed. Flume studies, particularly in tandem with well designed field experiments, could separate out the relative contributions of grain size, organic carbon and carbon flux, micro-organisms, "stability" (rigorously defined), larval supply, and hydrodynamics in creating species' distributions. Although reductionist approaches have numerous drawbacks, they are an important tool for untangling the existing web of ideas on animal-sediment relationships. We conclude by again stating that it may not be possible, in some cases, to decouple sediment versus flow versus sediment transport effects on organism distributions because these factors are so tightly coupled in nature. Rather than attempting to do so, it may be more fruitful to develop new theories and models that embrace the gestalt of the sedimentary milieu. Returning to the opening quote by Hutchinson (1953) regarding the concept of pattern in ecology we suggest that animal-sediment relationships probably are "a mere trivial expression of something we may learn to expect all the time", but it's that "something" that is yet to be identified!

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# CHAPTER 2

## Hydrodynamic Enhancement of Larval Settlement in the Bivalve *Mulinia lateralis* (Say) and the Polychaete *Capitella* sp. I in Microdepositional Environments

This chapter has been accepted for publication in Journal of Experimental Marine Biology and Ecology with Cheryl Ann Butman and Judith P. Grassle as co-authors.

## ABSTRACT

To test whether larval settlement patterns of the opportunistic bivalve Mulinia lateralis (Say) and the opportunistic polychaete Capitella sp. I are influenced by near-bottom flow, laboratory still-water and flume-flow experiments were conducted using a sediment-filled array consisting of depressions and compartments flush with the flume bottom. Compartments were filled with organic-rich mud or a low-organic, glass-bead mixture of a comparable grain size. Previous flume experiments have shown that larvae of both species settle in greater numbers in mud compared with glass beads. Depressions create a hydrodynamic environment that traps passive particles, permitting tests of the relative importance of active selection versus passive deposition of larvae in regions of microtopography. In both flow and still water, Capitella sp. I larvae consistently selected organic-rich mud over glass beads, regardless of whether treatments were flush or depressions. Settlement was higher, however, in depressions (3.8 cm in diameter and 2.8 cm deep) for a given sediment treatment, particularly in glass bead treatments in flow. In flow and still-water experiments, M. lateralis larvae also chose mud over glass beads but, in some instances, higher settlement occurred in glass bead depressions (a "poor" choice) compared to flush mud (a "good" choice). These results suggest that near-bottom flow influences settlement distributions of both species (i.e., settlement enhancement in depressions), but the effect may be greater for M. lateralis larvae. Higher settlement generally observed in mud depressions compared with glass bead depressions suggests that larvae of both species may have been able to "escape" from depressions if the substratum was unsuitable, although M. lateralis larvae were

poorer swimmers than Capitella sp. I larvae and were more vulnerable to passive entrainment and retention in depressions. Similar experiments with smaller depressions (9 mm in diameter and 9 mm deep) showed no settlement enhancement in depressions for Capitella sp. I and enhancement in only one of two flow experiments with M. lateralis larvae, suggesting that the hydrodynamic, trapping effect may be scale dependent for both species.

## INTRODUCTION

Many studies have documented the associations of soft-sediment invertebrates with specific sediment types (e.g., Gray, 1974; Rhoads, 1974), but much less progress has been made in determining the mechanisms responsible for such relationships. One explanation for animal-sediment associations is that near-bed hydrodynamics may sort some planktonic larvae in a way comparable to sediment sorting (e.g., Butman, 1987). Thus, organisms may be sediment specific in their distribution because the hydrodynamic factors that produced the sediment type in a given area may also influence whether or not larvae are deposited in that locale.

Habitat selection by larvae of infaunal invertebrates under realistic hydrodynamic conditions has been tested in very few species (Butman, 1987). Two species that have been examined in this respect are the polychaete Capitella sp. I and the bivalve Mulinia lateralis (Say). In laboratory still-water and flume-flow experiments, both Capitella sp. I (Butman et al., 1988b; Butman & Grassle, in press) and M. lateralis (Grassle et al., 1992) clearly chose high-organic mud over low-organic glass beads with a similar grain-size distribution. Larval delivery to the arrays appeared to be controlled largely by hydrodynamic processes, however, physically constraining the sediments to which the larvae were exposed. These experiments suggest that both passive physical processes and active biological behaviors ultimately determine settlement patterns in these species.

Given the opportunistic nature of these species, substrate-selective behavior is expected. Capitella sp. I has lecithotrophic larvae capable of settlement moments after

hatching (Dubilier, 1988) yet metamorphosis may be delayed for at least 5 days without significant mortality (Grassle, unpublished), decreased selectivity (Grassle et al., in press) or negative effects on post-metamorphic growth and fecundity (Pechenik & Cerulli, 1991). This species also rapidly colonizes disturbed organic-rich sediments (Grassle & Grassle, 1977). Similarly, Mulinia lateralis often appears suddenly in dense populations in organically enriched muds with relatively low oxygen content (Boesch, 1973; Oviatt et al., 1984; Walker & Tenore, 1984). Unlike Capitella sp. I, however, M. lateralis has planktotrophic larvae that may delay settlement for only a few days after attaining competency in approximately 10-12 days at 21° C (Grassle et al., 1992). In natural habitats, major settlement events for M. lateralis may be confined to time periods of only a few days (Luckenbach, 1984). Larval characteristics, distributions and population dynamics of these species thus suggest that they are more likely to be selective than species with, for example, less habitat affinity as adults and more extended competency periods (e.g., Bachelet et al., in press).

Although larvae of Mulinia lateralis and Capitella sp. I are capable of habitat selection at scales comparable to the size of the organisms, the effects of this selectivity on large-scale distribution patterns are not well understood. The swimming speeds of larvae of many infaunal species may be insufficient to overcome flow speeds that occur at distances more than several body lengths above the bottom (Butman, 1986a; Jonsson et al., 1991), suggesting that even selective larvae may be heavily influenced by near-bed hydrodynamics (Pawlik et al., 1991; Butman & Grassle, in press; Pawlik & Butman, submitted). Larvae may be horizontally advected like passive particles, intermittently

swimming or sinking out of suspension and testing the substrate. If the substrate is suitable, they may settle and/or metamorphose; otherwise they may simply move up off the bottom and be advected further downstream. At the other extreme, larvae may move around near the bottom independent of flow, searching for a suitable substrate. In the passive-transport scenario, larvae are completely dependent on bottom currents to bring them into contact with a suitable substrate. This would significantly affect where larvae settle, particularly if the competency period is limited.

There is, in fact, compelling evidence that larval settlement of at least some infaunal species may be influenced by near-bed hydrodynamics. The polychaete Phragmatopoma lapidosa californica, although ultimately metamorphosing in response to chemical cues (e.g., Pawlik, 1986; Jensen et al., 1990), settled in higher numbers in relatively fast versus slow flows (Pawlik et al., 1991). Subsequent experiments have identified an upper limit to steady unidirectional flows for which settlement and metamorphosis is physically possible in this species (Pawlik & Butman, submitted). Larvae of Mulinia lateralis appeared to actively select more consistently in flow than in still water (Grassle et al., 1992). Moreover, settlement distributions of Capitella sp. I larvae apparently can be affected by even relatively weak flows, such as the cross-stream circulation in a racetrack-design flume (Butman & Grassle, in press; see also Discussion of this paper). Several field studies suggest that near-bed hydrodynamics may be important determinants of recruitment patterns of benthic larval (e.g., Eckman, 1979, 1983; Savidge & Taghon, 1988; Butman, 1989) and post-larval macrofauna (Emerson & Grant, 1991), and meiofauna (Palmer & Gust, 1985; Kern & Taghon,

1986).

To test the importance of near-bed hydrodynamics in the settlement of Mulinia lateralis and Capitella sp. I larvae, laboratory still-water and flume-flow experiments were conducted using an array consisting of flush sediment treatments and small cylindrical depressions containing a comparable volume of sediment. Experiments were conducted with depressions of two sizes to determine whether any observed depression effect was scale dependent. The experimental design permitted tests of the relative importance of active habitat selection versus passive deposition. Settling larvae could, for example, be passively "trapped" and settle in the microdepositional environment of depressions, even where the substrate within the depressions was unsuitable. Alternatively, they could consistently choose a preferred substrate independent of near-bed flow effects, and thus occur in comparable numbers in flush and depression treatments containing a preferred sediment. These laboratory experiments with no suspended sediment eliminate the ambiguity of field experiments where enhanced settlement in depressions may result from passive accumulation in microdepositional environments or active selection by larvae for high organics or fine particles that are hydrodynamically concentrated in depressions (e.g., Savidge & Taghon, 1988).

Depressions in soft-sediment environments may be created through a variety of biological activities ranging from whale (e.g., Oliver & Slattery, 1985), fish (VanBlaricom, 1982), and crab feeding (e.g., Hall et al., 1991) to sediment reworking by deposit feeders (e.g., Nowell et al., 1984). Under some flow conditions, pits have been shown to contain elevated amounts of a variety of passive particles ranging from

coarse (Nelson et al., 1987) and fine (Risk & Craig, 1976) sediments to phytodetritus (Thiel et al., 1988) to macroalgae (Grassle & Morse-Porteous, 1987). The size and shape of depressions, along with flow and particle characteristics, determine trapping characteristics (e.g., Nowell & Jumars, 1984). The goal of this study was to use the passive-trapping environment of depressions to determine the susceptibility of competent larvae to near-bed hydrodynamics relative to their ability to selectively settle on a preferred substrate.

## MATERIALS AND METHODS

### LARVAL REARING

Adult Mulinia lateralis were obtained from Town Cove, Orleans, Massachusetts, USA in July, 1990 and February, 1991 and maintained in running sea water under conditions described by Grassle et al. (1992). Larvae were obtained by stripping gametes from at least five females and five males and then mixing oocytes and sperm until substantial fertilization was observed. At that time they were transferred to 30-l plastic barrels containing 21° C sea water filtered to 1 µm. Larvae were aerated and fed daily a mixture of two phytoplankton species, Pavlova lutheri and Isochrysis galbana at an approximate combined concentration of 50,000 cells•ml$^{-1}$, and sea water was changed every second day.

Larvae were examined every second day to determine size, stage of development and behavior. Contrary to our experience with the bivalve Mercenaria mercenaria

(Bachelet et al., in press), competency in Mulinia lateralis was fairly predictable and well defined; it could be roughly forecast 3-4 days in advance. On about day 10, monitoring of larvae for competency was increased to daily observations in an attempt to synchronize the experimental period with peak larval competency to settle. The larvae used in experiments were 10-13 days old. With experience, we learned that size and age were not always accurate predictors of physiological development and instead we used behavioral traits (cf. Coon et al., 1990). Thus, when spontaneous settlement and tumbling behavior (see Grassle et al., 1992) initially appeared, the flume was prepared for an experiment. When pediveligers were abundant and spontaneous settlement was observed in approximately 5% or more of a subsample of the culture, the population was considered competent, and the experiment was initiated.

Capitella sp. I larvae were obtained from brood tubes of adults from Grassle's stocks. Adult maintenance and larval handling techniques have been described elsewhere (Grassle & Grassle, 1976; Butman & Grassle, in press). To obtain a sufficient number of larvae for experiments, individuals from up to 20 broods were pooled and held in 15° C sea water without a settlement cue for a maximum of 72 h. Larvae were slowly brought up to flume temperature before the experiment began.

## COMPETENCY TESTS

For Mulinia lateralis, small-scale competency tests were often performed, either when competency appeared to be approaching (i.e., appearance of pediveligers) or once it had been determined from behavioral observations that the population was competent

and ready for the sediment-choice experiment (i.e., tumbling and the initial appearance of spontaneous settlement). Nine replicate dishes (4.5 cm diameter) were filled to a depth of 1 cm with sea water and a small patch (~1 cm diameter) of either New Bedford Harbor Mud (NBH Mud) or Glass Beads (both sediment treatments are described later) was added to each of three replicates. This resulted in three replicates each of NBH Mud, Glass Beads, or no substrate (Sea Water). Each replicate received ten swimming larvae chosen at random from the main culture. After 24 h, dishes were examined carefully and larvae were scored as swimming, metamorphosed, dead, or missing. This methodology is described in more detail in Grassle et al. (1992), and only results from a representative competency test will be presented here to demonstrate that our behavioral observations adequately predicted competency.

For Capitella sp. I, small-scale competency tests similar to those described above and in Butman et al. (1988b), Grassle & Butman (1989) and Butman & Grassle (in press) were run routinely and simultaneously with experiments to ensure that larvae were competent. Five larvae were placed in each of three replicate dishes containing the same treatments described above and dishes were examined at various intervals up to 90 minutes. Again, only representative data are presented here.

## THE FLUME AND SEDIMENT ARRAYS

Larval choice experiments were conducted in the Paddle-Wheel Flume at the Coastal Research Laboratory of Woods Hole Oceanographic Institution. The flume, which features recirculating, steady flow driven by plexiglass paddles, is described

elsewhere (Butman & Grassle, in press) with several exceptions unique to this study. The 6.1-m-long by 50-cm-wide straightaway, which contains the "test section" where experiments are normally conducted, was modified to allow for depressions in the flume floor. Four plexiglass panels fit snugly together to form the straightaway. The third section, however, could be removed and replaced with specially designed panels.

For most experiments, a panel with a built-in deep box (inner dimensions of 78.4 cm x 37.3 cm x 10.0 cm) replaced the third panel of the flume bottom. The upper size limit of the deep box was ultimately constrained by support girders under the flume, although boundary-layer considerations (see below) would likely have resulted in hydrodynamic problems with a larger box. The reason for the rectangular (rather than square, as in previous work) test section was to allow maximum downstream distance between treatments so that flow disturbances induced by depressions would be dissipated before the next treatment downstream. Width of the array was constrained by side-wall boundary-layer considerations (e.g., Nowell & Jumars, 1987). This deep box was modified to allow for flush and depression treatments.

A single piece of plexiglass (0.635 cm thick) was cut to fit snugly inside the box, flush with the floor of the flume. Sixteen holes (diameter 4.4 cm) were drilled in a uniform pattern over the plexiglass (Fig. 1a). Plexiglass tubes were placed in each hole with one end open and one end sealed so that the open end was flush with the plexiglass and flume floor. Eight of the tubes were 1 cm deep and eight were 3.8 cm deep. Distribution of tubes was again randomly determined but with two shallow and two deep depressions in each row and column. Sediment was added to fill the shallow tubes so

that they were flush with the floor of the flume, and a similar volume of sediment was added to the deep tubes to produce a depression 3.8 cm in diameter and 2.8 cm deep with a 1-cm deep layer of sediment in the bottom (Fig. 1b). This resulted in depressions with an aspect ratio (height/inside diameter) of 0.7. This array was used for the majority of the Capitella sp. I and Mulinia lateralis experiments (hereafter referred to as Capitella and Mulinia Main Array experiments). In total, four flow and three still-water experiments were conducted for each species using this array.

Several experiments (hereafter referred to as Capitella and Mulinia Small Array experiments) were conducted to determine whether depression effects might be scale dependent. These experiments used a four-by-four-compartment array described in Grassle et al. (in press) and Grassle et al. (1992). This array, which also fits flush with the flume bottom, has outer dimensions of 28.5 cm x 28.5 cm and 16 circular sediment compartments 4.5 cm in diameter and 1 cm deep (Fig. 2). Small depressions were made in half of the compartments by inserting a piece of glass tubing (9 mm inner and 10 mm outer diameter, 1 cm deep) with one end sealed with Parafilm and the other end open. Sediment was added to the areas around the tubing and to the compartments without tubes so that sediment was flush with the bottom of the flume. A very thin layer of sediment was placed in the bottom of the tubes, producing a depression 9 mm in diameter and approximately 9 mm deep (aspect ratio of 1.0). Larval settlement choice experiments conducted using this array included one in flow and one in still-water for Capitella sp. I larvae and two in flow and two in still water for M. lateralis larvae.

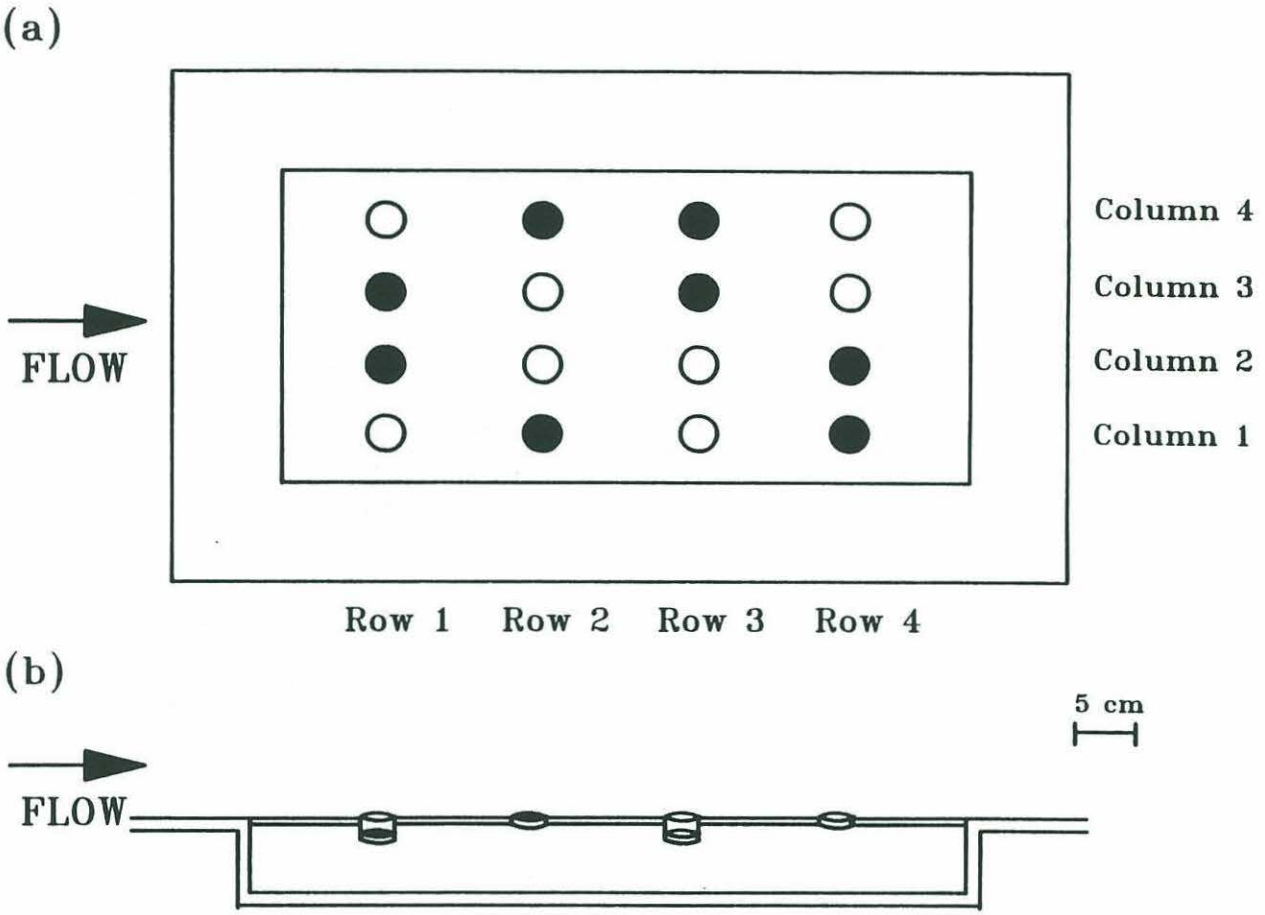


Figure 1. (A) Top view diagram of Main Array. Solid circles denote NBH Mud treatments and clear circles denote Glass Beads treatments. The diameter of each compartment is 3.8 cm. (B) Side view of Main Array showing flush and depression compartments with solid areas indicating NBH Mud and clear compartments indicating Glass Beads.

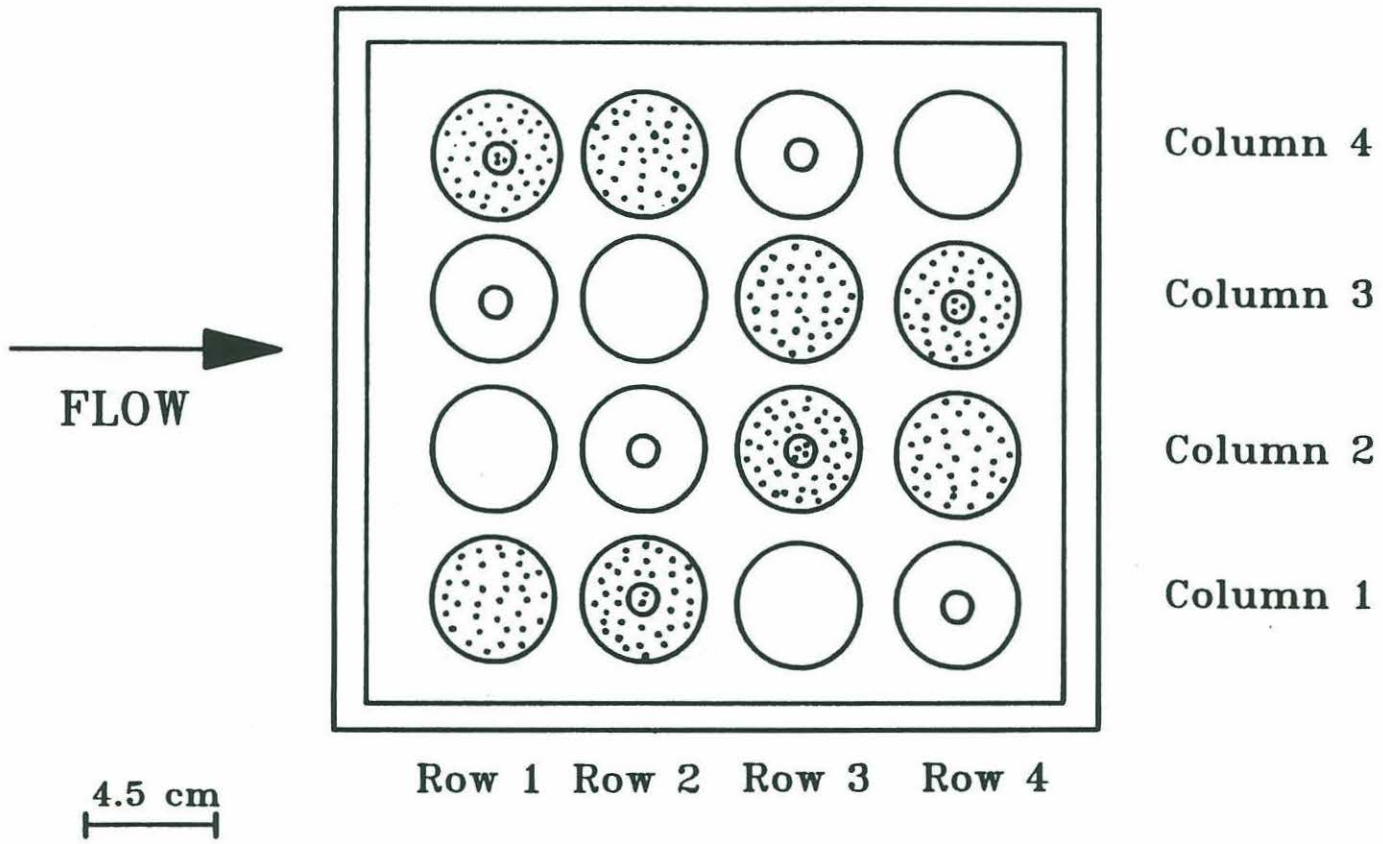


Figure 2. Top view diagram of the Small Array. Smallest circles denote depressions (9 mm diameter) filled with NBH Mud or Sipp Mud (stippled) or Glass Beads or Nobska Sand (clear). Larger circles denote entire compartments (45 mm diameter) that were filled with the same types of sediment.

SEDIMENT TREATMENTS

The same two sediment treatments were used in all experiments, except for the Mulinia Small Array experiments. As in Butman et al. (1988b), Grassle & Butman (1989), Bachelet et al. (in press), and Butman & Grassle (in press), the two sediments differed greatly in organic content to increase the likelihood of observing a clear selection response. One sediment treatment was an organic-rich mud collected from outer New Bedford Harbor (hereafter referred to as NBH Mud), which is known to elicit higher settlement and metamorphosis of Mulinia lateralis (Grassle et al., 1992) and Capitella sp. I (Butman et al., 1988b; Butman & Grassle, in press) larvae than a low-organic alternative. The second sediment treatment was a glass bead mixture with extremely low organic content that is known to be less attractive to both species. The NBH Mud (typical ratios of the percentages of organic carbon, hydrogen, nitrogen, or C:H:N, of 3.37:0.68:0.32, Bachelet et al., in press), was collected from 10 m depth in outer New Bedford Harbor using a van Veen grab; the top 2-3 cm of mud was pushed through a 1 mm sieve and frozen prior to thawing the day an experiment was to be set up. The glass-bead mixture (typical C:H:N values 0.1:0.1:0, Bachelet et al., in press), which has a grain-size distribution roughly comparable to that of the NBH Mud (i.e., both treatments ~ 70% of the particles < 63 µm; Bachelet et al., in press), was produced by thoroughly mixing three size classes of Ferro Class IVA Microbeads; 40% 13-44 µm, 30% 53-74 µm, and 30% 88-125 µm. The glass-bead mixture (hereafter referred to as Glass Beads) was then thoroughly washed in filtered sea water, frozen and later thawed, along with the mud, as needed.

Two sediment types were used with flush or depression compartments, resulting in four treatments: Flush NBH Mud, NBH Mud Depressions, Flush Glass Beads and Glass Beads Depressions. A Latin squares design was used for all experiments, with one treatment in each row and column. Treatments were randomly allocated with the constraint that the locations of depressions in each row and column were fixed and thus could not be completely randomized. The array was rotated 180° for some experiments and later rebuilt to relocate depressions, thereby increasing the combinations of treatment locations.

The Capitella Small Array experiments used the sediment treatments described above. For Mulinia Small Array experiments, however, two natural sediments were used. The two sediment choices were an organic-rich mud (Sipp Mud) collected from Sippewissett Marsh, West Falmouth, Massachusetts and a relatively low-organic sand (Nobska Sand) collected above high water at Nobska Beach, Falmouth, Massachusetts. Unlike the Main Array experiments, the grain size distributions and the organic content differed substantially between sediment types. Nobska Sand was collected dry and never frozen. Sipp Mud was treated as described for NBH Mud. A Latin squares design was also used for these experiments.

## EXPERIMENTAL PROTOCOL

On the day prior to an experiment, the experimental arrays were filled with the appropriate sediment treatments. The flume was filled to 10 cm depth with 1-µm-filtered sea water pumped from Vineyard Sound, Massachusetts. To eliminate sediment

suspension, sediment areas were covered with weighted caps which were removed only when the water level was well above the flume bottom. The uncapped array was left in the flume overnight before beginning the experiment the following day. In order to replicate conditions as much as possible between flow and still water, the Main Array still-water experiments were also conducted in the flume. Furthermore, the still-water experiments served as controls for potential flow modification of depressions relative to flush treatments (e.g., accumulation in depressions of organic matter that passed through the 1 μm filter). Therefore, for Capitella Still 2 and 3 and Mulinia Still 2 and 3 (numbers refer to experiments as described later, see Tables III and V), the flume ran for 4 h and was then stopped before beginning an experiment. Prior to adding larvae, panels were placed vertically in the flume to confine larvae to the area of the flume directly above the test section. For Capitella and Mulinia Still 1, the flume was not run prior to the experiments, but the vertical panels were again used to confine larvae.

The Small-Array experiments were conducted slightly differently. The small array was filled, covered with a sealing lid, and then gently lowered into the flume. The lid was removed, and the array was left overnight before the experiment. A 50 cm x 50 cm still-water box, described in detail by Bachelet et al. (in press) was used for the still-water Small Array experiments. As in the flume, the array fit snugly in the bottom of the box to create a flush surface. Water depth was 10 cm to duplicate that in the flume.

Water temperature was generally close to 20° C, and was heated to this temperature in winter. Heaters were removed once the water was sufficiently warm, and

the water was recirculated for at least 30 min to allow thorough mixing before larvae were added. Although heaters were not present during the experiments, water temperature did not drop more than 2° C during a winter experiment.

In Mulinia Flow 4, cultured algae was added to evaluate whether results could be affected by the fact that planktotrophic larvae were not fed during the 24-h period of the experiment. Thus, a mixture of Isochrysis galbana and Pavlova lutheri was introduced downstream of the paddle wheel and given sufficient time to mix throughout the water before larval addition. Algal concentration was chosen to match that used in larval rearing (see below).

All flow experiments were conducted using the moderately slow, turbulent flow described by Butman & Grassle (in press). Mean horizontal velocity at 7 cm above the bottom was approximately 5 $cm \cdot s^{-1}$, and boundary shear velocity ($u_*$), was approximately 0.26 $cm \cdot s^{-1}$ as calculated from detailed velocity profiles (Butman & Grassle, in press). This corresponds to a $u_*$ which is in the mid-range for tidal flow in a typical coastal embayment (e.g., range of $u_*$ for tidal flows in Buzzards Bay is 0 to 0.60 $cm \cdot s^{-1}$; Butman, 1986a).

Once a sufficient number of Capitella sp. I broods had hatched or Mulinia lateralis larvae were judged to be competent, an experiment was begun. Healthy, non-metamorphosed Capitella sp. I larvae were counted and placed into four equal aliquots. Mulinia lateralis larvae were concentrated from 30 l into a smaller volume (1-2 l) before estimating density from a subsample; larvae were then divided into four containers. For both species, the number of larvae used was generally dictated by the number available,

and therefore varied between experiments. Polystyrene spheres (Duke Scientific DVB microspheres, density of 1.05 $g \cdot cm^{-3}$, diameter of 383 ± 8 μm; hereafter referred to as spheres) were added as passive larval mimics. Three hundred spheres were added to each of the larval aliquots (1200 total spheres). Non-random distribution of spheres in the sediment array would indicate either bias in the way aliquots were added or a depression trapping effect.

For flow experiments, larvae and spheres were added in the straightaway upstream of the array to increase the probability that they would encounter the sediments during their first pass. Larvae and spheres were added together, 1 cm below the surface of the water, at two points approximately 3 and 4 m upstream of the first row of compartments (two aliquots at each point). These upstream points were chosen somewhat arbitrarily because addition location apparently did not affect recovery of larvae and spheres in the array (Butman & Grassle, in press).

For still-water experiments, larvae and spheres were divided into four aliquots and (carefully and slowly) poured directly over the array while moving the container from side to side. One aliquot was poured over one of each of the four rows, to try to create a relatively homogeneous distribution of larvae in the water column. For still-water experiments with the small array, larvae were divided into 16 equal aliquots and introduced 1 cm below the water surface over each of the compartments (see Grassle et al., 1992).

Mulinia lateralis experiments were run for 24 h because 4-h, small-scale competency tests produced relatively low settlement and metamorphosis. Capitella sp.

I experiments ran for 4 h. Previous experiments and small-scale competency tests with Capitella sp. I (Butman & Grassle, in press) showed substantial settlement in 2 h. Experimental duration was doubled here in an attempt to compensate for the wide spacing between treatments by increasing the potential number of larval passes over the array.

For the Main Array experiments, weighted caps were placed over each of the 16 compartments before draining the flume as quickly as possible. The area around the compartments was sponged dry, caps were removed, and the fluid and sediment from the compartments were carefully removed and preserved.

The same sealing lid used for inserting the small array in the flume was locked in place before removing the small array from the flume (or still-water box). The sediment was carefully removed from each of the compartments. For Main and Small Array experiments, samples were preserved in 10% buffered formalin and later transferred to 90% ethanol with Rose Bengal stain. Mulinia lateralis samples were placed directly into ethanol to reduce shell dissolution (e.g., see Bachelet et al., in press).

SWIMMERS VS. SETTLERS

For several of the experiments, we attempted to determine what proportion of the individuals collected in the array had settled and/or metamorphosed. In previous experiments with Capitella sp. I (Butman et al., 1988b; Butman & Grassle, in press; Grassle et al., in press), individuals were enumerated live so that it was possible to be

certain that all individuals had metamorphosed. This was logistically impossible for our experiments and there may have been non-metamorphosed individuals counted as settled juveniles. This is particularly true for individuals that were entrained in depressions but did not necessarily metamorphose. The same problem may exist for Mulinia lateralis larvae. Therefore, for several experiments with each species, unpreserved samples from the array were quickly washed over a 74-µm sieve and returned to sea water. Each sample was observed for 5 min to determine how many swimming larvae remained. Following this procedure, samples were preserved and later enumerated under a dissecting microscope. Because proportions of swimmers were fairly consistent among different experiments, results are presented here only from single, representative experiments.

## HYPOTHESES FOR SELECTION EXPERIMENTS

All of the selection experiments were designed to test the hypothesis that larvae of Mulinia lateralis and Capitella sp. I (or spheres) are deposited on the bottom as passive particles and should, therefore, occur in higher numbers in depressions compared with flush sediment, regardless of sediment type. That is, passively deposited larvae (or spheres) should occur in comparable numbers in Flush NBH Mud and Flush Glass Beads treatments, but in substantially higher numbers in NBH Mud Depressions and Glass Beads Depressions.

STATISTICAL ANALYSES OF SELECTION EXPERIMENTS

Overall larval settlement patterns in the Capitella and Mulinia Main Array experiments were analyzed using the partial hierarchical ANOVA model $y = \mu + Flow + Batch(Flow) + Row + Column + Treatment + Flow \times Treatment + Flow \times Row + Flow \times Column + Batch(Flow) \times Treatment + Batch(Flow) \times Row + Batch(Flow) \times Column + Error$, where $\mu$ is a constant, Flow is the flow/still-water contrast, and Batch is the batch of larvae nested within Flow. Batch refers to larvae from a single spawning of at least 10 adult clams on a given date for each Mulinia lateralis experiment, or the combined broods of larvae used for each of the Capitella sp. I experiments. Treatment is the main effect (i.e., testing for differences between NBH Mud Depressions, Glass Beads Depressions, Flush NBH Mud, and Flush Glass Beads) and Row and Column are blocking factors to account for location of replicate treatment compartments. Row and Column terms were included because we have observed that spatial location of compartments can be an important source of settlement variance (e.g., Butman & Grassle, in press; Grassle et al., in press). All terms in the model were fixed except Batch, which was random. When F-tests indicated heteroscedasticity, data were log (x+1) transformed to homogenize variances between treatments. For Capitella sp. I, all four flow experiments and three still-water experiments were included in the analysis. For M. lateralis, Mulinia Flow 4 was excluded from the analysis because of the potentially confounding factor of food addition; thus, the analysis included three flow experiments and three still-water experiments. When significant differences were observed for any of the main effects comparisons, Tukey's HSD Multiple Comparisons

tests were performed to determine which means differed. This statistical design assumes independence among batches of larvae, but we used the same batch of larvae for Mulinia Flow 2 and Mulinia Still 1, and a different batch for Mulinia Still 2 and Mulinia Still 3. Because larvae in both cases were different ages at the times of the experiments, we assume that they were no more similar than two different batches of larvae, and therefore they were treated as independent experiments.

Because sphere recovery in Capitella and Mulinia Main Array Flow experiments was generally < 2%, only data from the still-water experiments were analyzed with the ANOVA model $y = \mu + Batch + Treatment + Row + Column + Batch \times Treatment + Batch \times Row + Batch \times Column + Error$. Again, data were log (x+1) transformed when necessary to eliminate problems of heteroscedasticity. When the analysis indicated significant Treatment differences, and no significant Treatment x Batch interaction, Treatments within each experiment were averaged and compared over replicate experiments using Tukey's tests. Sphere recovery was > 2% in Mulinia Flow 2 and Mulinia Flow 4; each experiment was analyzed as a separate Latin square using the ANOVA model $y = \mu + Treatment + Row + Column + Error$.

Because individual Mulinia and Capitella Small Array experiments were not directly comparable to the Main Array, data were analyzed separately using the Latin squares ANOVA model $y = \mu + Treatment + Row + Column + Error$. Data were log (x+1) transformed when F-tests indicated heteroscedasticity. When significant differences were observed for any of the main effects, Tukey's HSD Multiple Comparisons tests were performed to determine which Treatments, Rows or Columns

differed.

## RESULTS

### COMPETENCY

Most Capitella sp. I larvae settled and metamorphosed very rapidly (5-30 min) when exposed to NBH Mud (Fig. 3). Few individuals settled and metamorphosed when a suitable substrate was absent (i.e. Sea Water or Glass Beads treatments), even after 90 min. Results of all of the competency tests conducted in conjunction with each of the Capitella sp. I experiments were similar to these results, indicating that larvae used in all experiments were competent and healthy.

Competency tests were performed less frequently for Mulinia lateralis because late-stage pediveligers often "rested" on the bottom without necessarily metamorphosing, making evaluation of competency difficult. Furthermore, in many of the competency tests we were unable to locate all ten of the larvae that had been added to each dish. In the case of NBH Mud treatments, this was probably because some larvae settled and could not be relocated in the mud without staining the larvae, or greatly increasing the observation time. Therefore, we relied more on behavioral observations of larvae in a subsample of the culture to decide when the population was competent. The presence of large numbers of pediveligers and onset of low levels of spontaneous settlement and metamorphosis suggested to us that a significant portion of the culture was competent to settle.

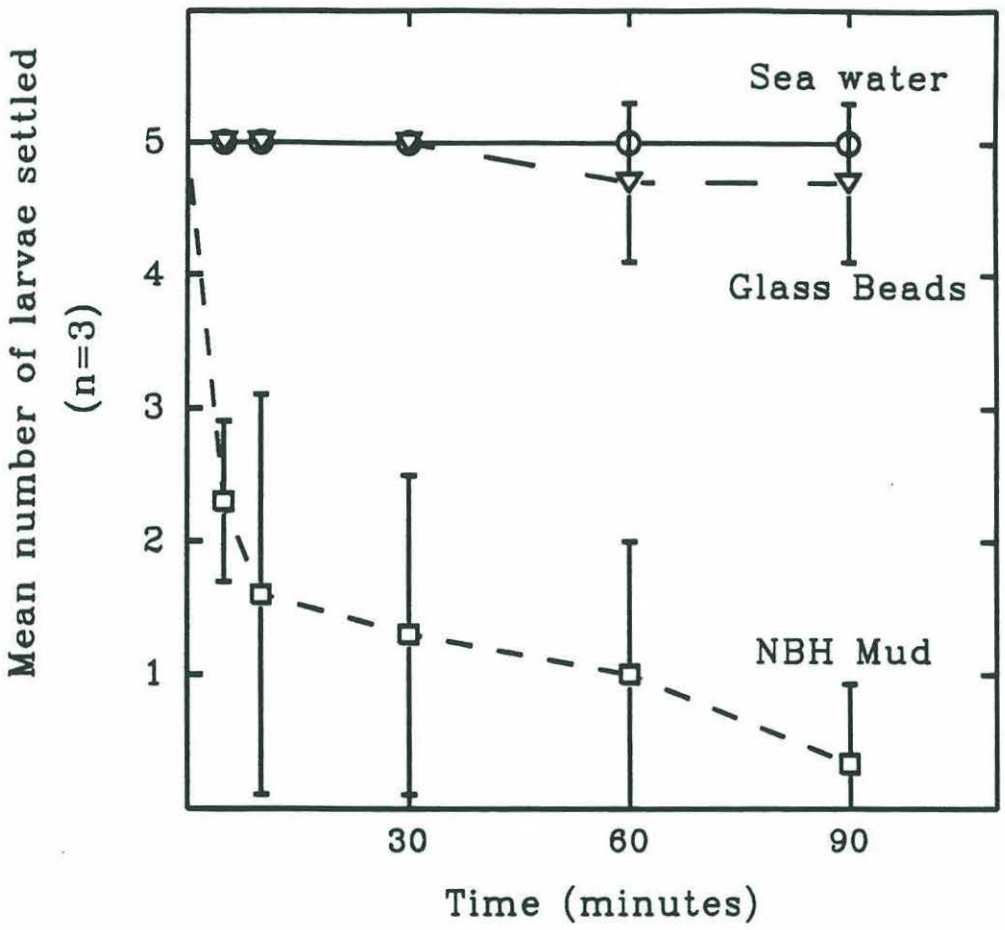


Figure 3. Results of Capitella sp. I competency tests conducted simultaneous with Capitella Flow 2. Five larvae were added to each dish. Points denote means (n=3) and lines denote 1 standard deviation.

A representative time series of competency tests is shown for larvae used in Mulinia Flow 2 and Mulinia Still 1 (Table I). Before day 11, very few larvae had metamorphosed after 24 h, regardless of treatments, suggesting that most larvae were not yet competent. The number of metamorphosed larvae was highest in the competency test for day 12 larvae, which was the test that ran simultaneously with Mulinia Flow 2. Some spontaneous metamorphosis occurred by days 14 and 15, the latter being coincident with Mulinia Still 1. Nonetheless, more larvae settled in NBH Mud, and a significant proportion of the individuals were still swimming in the Glass Beads and Sea Water dishes in the day 15 test.

## GENERAL OBSERVATIONS

All Capitella experiments were conducted for 4 h and at temperatures between 17 and 24° C (Table II), but larval recovery in the array was variable (Table III). Recovery of larvae in Capitella Main Array experiments varied from 12.4% to 31.0% in flow and from 6.5% to 28.5% in still water. These percentages are roughly within the range of those found in previous 2-h, flow experiments using these same two same sediment treatments (i.e., recoveries of 9.3%-26.6% in Butman & Grassle, in press). Percentages of Capitella sp. I larvae recovered in the still-water arrays, however, were lower than those found previously (i.e., 61.1%-64.5% in Butman & Grassle, in press). Differences in number of larvae added (Table II), batch-to-batch variation in larvae, and variation in experimental conditions may all have influenced recovery. Presumably, those individuals that were not recovered in the array were either swimming or had

TABLE I

Twenty-four hour competency tests associated with Mulinia Flow 2 and Mulinia Still 1. Numbers given are out of 10 larvae added per replicate. Totals do not necessarily add to 10 because in some instances not all larvae were recovered (see text).

| Larval Age | Sediment Treatment | Number of Swimmers ($\bar{x}$±1sd, n=3) | Number of Tumblers ($\bar{x}$±1sd, n=3) | Number Metamorphosed ($\bar{x}$±1sd, n=3) |
|---|---|---|---|---|
| Day 9 | NBH Mud | 8.7±2.3 | 0.3±0.6 | 0.0±0.0 |
| | Glass Beads | 10.0±0.0 | 0.3±0.6 | 0.0±0.0 |
| | Sea Water | 9.3±1.2 | 0.3±0.6 | 0.0±0.0 |
| Day 10 | NBH Mud | 6.3±1.2 | 0.7±0.6 | 1.3±1.5 |
| | Glass Beads | 9.3±1.2 | 0.7±1.2 | 0.0±0.0 |
| | Sea Water | 8.3±0.6 | 1.3±0.6 | 0.0±0.0 |
| Day 11 | NBH Mud | 2.7±2.1 | 1.3±1.5 | 3.7±1.5 |
| | Glass Beads | 8.0±3.6 | 4.3±1.5 | 0.3±0.6 |
| | Sea Water | 6.7±1.5 | 1.7±1.5 | 0.3±0.6 |
| Day 12 | NBH Mud | 1.0±0.0 | 0.0±0.0 | 7.3±1.5 |
| | Glass Beads | 6.7±1.5 | 0.7±0.6 | 0.0±0.0 |
| | Sea Water | 7.3±1.2 | 1.0±1.0 | 0.0±0.0 |
| Day 13 | NBH Mud | 1.0±1.7 | 0.3±0.6 | 5.0±1.0 |
| | Glass Beads | 5.3±1.2 | 1.7±1.2 | 3.0±0.0 |
| | Sea Water | 5.7±0.6 | 3.7±1.2 | 0.7±0.6 |
| Day 15 | NBH Mud | 0.7±1.2 | 0.3±0.6 | 6.3±0.6 |
| | Glass Beads | 3.7±1.5 | 2.7±0.6 | 2.7±0.6 |
| | Sea Water | 5.0±3.6 | 1.7±0.6 | 2.7±3.1 |

TABLE II
Conditions for Capitella sp. I experiments.
All experiments ran for 4 h.

| Experiment | Date | Temp. (°C) | Number added |
|---|---|---|---|
| **Main Array** | | | |
| Flow 1 | 6-6-91 | 18.4 | 6000 |
| Flow 2 | 7-25-91 | 24.0 | 4200 |
| Flow 3 | 8-6-91 | 22.8 | 4200 |
| Flow 4 | 8-8-91 | 23.0 | 3900 |
| Still 1 | 8-23-91 | 22.9 | 3000 |
| Still 2 | 9-16-91 | 22.0 | 3000 |
| Still 3 | 9-18-91 | 22.1 | 3000 |
| **Small Array** | | | |
| Flow A | 4-5-91 | 17.3 | 3000 |
| Still A | 4-7-91 | 19.4 | 3000 |

TABLE III

Mean number of larvae and spheres collected per treatment in all Capitella experiments. NBH refers to New Bedford Harbor Mud, GB refers to Glass Beads.

| | Sediment Treatment | Number of Larvae ($\bar{x}$±1sd) | Total Number of Larvae Recovered (% of Total) | Number of Spheres ($\bar{x}$±1sd) | Total Number of Spheres Recovered (% of total) |
|---|---|---|---|---|---|
| **Main** | **Flow 1** | | 739 (12.3) | | 22 (1.8) |
| **Array** | NBH Depression | 91.8±46.7 | | 3.0±2.3 | |
| | GB Depression | 18.8±3.6 | | 0.8±1.0 | |
| | NBH Flush | 67.0±51.5 | | 0.8±1.0 | |
| | GB Flush | 7.2±5.4 | | 1.0±0.8 | |
| | **Flow 2** | | 1304 (31.0) | | 17 (1.4) |
| | NBH Depression | 137.0±82.5 | | 1.8±2.2 | |
| | GB Depression | 20.8±5.7 | | 1.5±2.4 | |
| | NBH Flush | 167.5±69.2 | | 0.8±0.5 | |
| | GB Flush | 0.8±1.0 | | 0.2±0.5 | |
| | **Flow 3** | | 675 (16.1) | | 16 (1.3) |
| | NBH Depression | 108.8±60.5 | | 2.8±4.9 | |
| | GB Depression | 5.2±3.6 | | 0.2±0.5 | |
| | NBH Flush | 54.5±28.5 | | 0.8±1.0 | |
| | GB Flush | 0.2±0.5 | | 0.2±0.5 | |
| | **Flow 4** | | 484 (12.4) | | 14 (1.2) |
| | NBH Depression | 85.2±46.9 | | 0.8±1.0 | |
| | GB Depression | 4.75±3.1 | | 1.5±0.6 | |
| | NBH Flush | 30.8±11.6 | | 1.0±2.0 | |
| | GB Flush | 0.2±0.5 | | 0.2±0.5 | |
| | **Still 1** | | 195 (6.5) | | 71 (5.9) |
| | NBH Depression | 122.0±41.6 | | 8.0±3.9 | |
| | GB Depression | 10.0±3.2 | | 3.2±1.7 | |
| | NBH Flush | 58.5±11.0 | | 2.8±2.9 | |
| | GB Flush | 4.5±0.6 | | 3.8±2.8 | |

TABLE III (cont.)
Mean number of larvae and spheres collected per treatment in all Capitella experiments. NBH refers to New Bedford Harbor Mud, GB refers to Glass Beads.

| | Sediment Treatment | Number of Larvae ($\bar{x}$±1sd) | Total Number of Larvae Recovered (% of Total) | Number of Spheres ($\bar{x}$±1sd) | Total Number of Spheres Recovered (% of total) |
|---|---|---|---|---|---|
| **Main** | **Still 2** | | 746 (24.9) | | 104 (8.7) |
| **Array** | NBH Depression | 63.5±27.3 | | 11.8±10.3 | |
| **(cont.)** | GB Depression | 50.8±25.1 | | 4.8±4.2 | |
| | NBH Flush | 57.2±33.2 | | 7.8±6.1 | |
| | GB Flush | 15.0±16.7 | | 1.8±2.1 | |
| | **Still 3** | | 855 (28.5) | | 72 (6.0) |
| | NBH Depression | 81.0±22.3 | | 6.5±2.4 | |
| | GB Depression | 38.8±6.9 | | 6.8±3.5 | |
| | NBH Flush | 82.2±46.2 | | 2.5±0.6 | |
| | GB Flush | 11.8±9.9 | | 2.2±2.9 | |
| **Small** | **Flow A** | | 189 (6.3) | | |
| **Array** | NBH Depression | 30.2±27.7 | | No Spheres Added | |
| | GB Depression | 1.2±1.9 | | | |
| | NBH Flush | 31.0±27.6 | | | |
| | GB Flush | 0.50±0.58 | | | |
| | **Still A** | | 2079 (69.3) | | 230 (19.2) |
| | NBH Depression | 258.8±23.6 | | 11.0±10.2 | |
| | GB Depression | 21.5±8.5 | | 23.0±11.9 | |
| | NBH Flush | 223.2±58.5 | | 17.2±4.4 | |
| | GB Flush | 16.5±10.2 | | 6.2±3.6 | |

settled elsewhere in the flume or portion of the flume sealed off for still-water experiments, perhaps in response to small clumps of organic matter.

Efforts to maintain similar, constant conditions among replicate Mulinia Main Array experiments were modestly successful (Table IV), and recovery of Mulinia lateralis larvae was less variable (4.9% to 6.3% in flow and 3.9% to 11.9% in still water, Table V) than for Capitella sp. I larvae. Percentages of M. lateralis larvae recovered in the Main Array experiments were within the range of recoveries in other 24-h flow experiments (1.9-9.3%) but, like the Capitella experiments, recoveries of M. lateralis larvae in still water were generally lower than in other 24-h still-water experiments (9.6-30.6) (Grassle et al., 1992; ranges given here are for experiments where food was added; when no food was added, recoveries were 1.3% in flow and 26.0% in still water). Lower recoveries in still-water Main Array experiments compared with previous still-water results may reflect the larger array and more dispersed distribution of treatments.

For the Capitella Small Array experiments (Table III) and Mulinia Small Array experiments (Table V), recovery was generally less in flow and greater in still water compared with flow and still-water Main Array experiments. This is likely because the sediments in the smaller array occupied a more confined surface area. This may have presented a smaller "target" in flow, but not in still water where larvae were added directly above the array.

TABLE IV
Conditions for Mulinia lateralis experiments.
All experiments ran for 24 h.

| Experiment | Date | Temp (°C) | Larval Age (Days) | Food Added? | Size (µm) | Number Added |
|---|---|---|---|---|---|---|
| **Main Array** | | | | | | |
| Flow 1 | 06-14-91 | 19.4 | 11 | No | 200 | 50,000 |
| Flow 2 | 08-17-91 | 23.8 | 12 | No | 190* | 40,000 |
| Flow 3 | 01-12-92 | 16.8 | 12.5 | No | 200* | 20,000 |
| Flow 4 | 07-21-91 | 24.0 | 10 | Yes | 170* | 30,000 |
| Still 1 | 08-20-91 | 23.1 | 13 | No | 220* | 19,300 |
| Still 2 | 10-13-91 | 21.2 | 12 | No | 170 | 25,000 |
| Still 3 | 10-15-91 | 22.4 | 14 | No | 190 | 13,500 |
| **Small Array** | | | | | | |
| Flow A | 12-01-90 | 20.5 | 11 | No | 260 | 10,000 |
| Flow B | 12-13-90 | 19.5 | 10 | No | 270 | 10,000 |
| Still A | 12-01-90 | 21.0 | 11 | Yes | 260 | 10,000 |
| Still B | 12-13-90 | 22.0 | 10 | No | 270 | 10,000 |

*indicates mean larval shell length estimated from measurements on previous day

TABLE V

Mean number of larvae and spheres collected per treatment in all Mulinia lateralis experiments. NBH refers to New Bedford Harbor Mud, GB refers to Glass Beads. "Dep." signifies depressions.

| Experiment | Sediment Treatment | Number of Larvae ($\bar{x}$±1sd) | Total Number of Larvae Recovered (% of added) | Number of Spheres ($\bar{x}$±1sd) | Total Number of Spheres Recovered (% of added) |
|---|---|---|---|---|---|
| **Main** | **Flow 1** | | 2428 (4.9) | | 17 (1.4) |
| **Array** | NBH Depression | 265.8±103.9 | | 1.5±1.9 | |
| | GB Depression | 246.2±46.4 | | 1.8±1.3 | |
| | NBH Flush | 68.2±22.8 | | 0.5±1.0 | |
| | GB Flush | 26.8±15.0 | | 0.5±1.0 | |
| | **Flow 2** | | 2512 (6.3) | | 48 (4.0) |
| | NBH Depression | 554.8±124.3 | | 2.8±3.1 | |
| | GB Depression | 38.0±21.4 | | 2.0±2.8 | |
| | NBH Flush | 27.5±7.5 | | 6.0±9.3 | |
| | GB Flush | 7.8±9.6 | | 1.2±1.0 | |
| | **Flow 3** | | 988 (4.9) | | 18 (1.5) |
| | NBH Depression | 133.2±42.7 | | 2.2±2.6 | |
| | GB Depression | 79.8±53.7 | | 1.8±1.5 | |
| | NBH Flush | 31.5±16.3 | | 0.5±0.6 | |
| | GB Flush | 2.5±1.7 | | 0.0±0.0 | |
| | **Flow 4** | | 1774 (5.9) | | 142 (11.8) |
| | NBH Depression | 280.5±65.2 | | 10.5± 1.9 | |
| | GB Depression | 116.5±86.7 | | 18.2± 6.3 | |
| | NBH Flush | 37.8±8.5 | | 3.2±2.9 | |
| | GB Flush | 8.8±5.7 | | 3.5±1.3 | |
| | **Still 1** | | 2293 (11.9) | | 82 (6.8) |
| | NBH Depression | 356.5±101.2 | | 6.5±3.7 | |
| | GB Depression | 63.0±13.0 | | 5.2±1.9 | |
| | NBH Flush | 112.5±21.4 | | 3.5±2.1 | |
| | GB Flush | 41.25±10.7 | | 5.2±3.5 | |

TABLE V (cont.)
Mean number of larvae and spheres collected per treatment in all Mulinia lateralis experiments. NBH refers to New Bedford Harbor Mud, GB refers to Glass Beads. "Dep." signifies depressions.

| Experiment | Sediment Treatment | Number of Larvae ($\bar{x}$±1sd) | Total Number of Larvae Recovered (% of Added) | Number of Spheres ($\bar{x}$±1sd) | Total Number of Spheres Recovered (% of Added) |
|---|---|---|---|---|---|
| **Main** | **Still 2** | | 981 (3.9) | | 71 (5.9) |
| **Array** | NBH Depression | 90.0±37.3 | | 6.8±5.1 | |
| | GB Depression | 108.0±10.3 | | 6.0±4.8 | |
| | NBH Flush | 32.2±9.7 | | 3.8±3.6 | |
| | GB Flush | 15.0±5.2 | | 1.2±0.5 | |
| | **Still 3** | | 1032 (7.6) | | 64 (5.3) |
| | NBH Depression | 90.5±18.7 | | 5.5±2.6 | |
| | GB Depression | 97.5±22.6 | | 5.5±2.6 | |
| | NBH Flush | 40.0±18.3 | | 3.0±1.6 | |
| | GB Flush | 30.0±14.3 | | 2.0±1.8 | |
| **Small** | **Flow A** | | 335 (3.4) | | 10 (0.8) |
| **Array** | Sipp Mud Dep. | 20.5±3.5 | | 0.2±0.5 | |
| | Nobska Dep. | 32.2±5.1 | | 0.5±0.6 | |
| | Sipp Mud Flush | 7.5±3.3 | | 0.8±1.0 | |
| | Nobska Flush | 23.5±4.5 | | 1.0±1.4 | |
| | **Flow B** | | 298 (3.0) | | 45 (3.8) |
| | Sipp Mud Dep. | 20.8±1.9 | | 3.2±1.9 | |
| | Nobska Dep. | 30.0±21.5 | | 2.0±2.2 | |
| | Sipp Mud Flush | 12.0±9.2 | | 1.8±1.7 | |
| | Nobska Flush | 22.0±2.6 | | 4.2±4.4 | |

TABLE V (cont.)
Mean number of larvae and spheres collected per treatment in all Mulinia lateralis experiments. NBH refers to New Bedford Harbor Mud, GB refers to Glass Beads. "Dep." signifies depressions.

| Experiment | Sediment Treatment | Number of Larvae ($\bar{x}$±1sd) | Total Number of Larvae Recovered (% of Added) | Number of Spheres ($\bar{x}$±1sd) | Total Number of Spheres Recovered (% of Added) |
|---|---|---|---|---|---|
| **Small** | **Still A** | | 2375 (23.8) | | 274 (22.8) |
| **Array** | Sipp Mud Dep. | 133.5±55.8 | | 14.5±9.2 | |
| | Nobska Dep. | 205.0±46.2 | | 19.0±1.4 | |
| | Sipp Mud Flush | 68.5±16.0 | | 14.5±7.1 | |
| | Nobska Flush | 186.8.±42.6 | | 20.5±8.4 | |
| | **Still B** | | 4525 (45.2) | | 499 (41.6) |
| | Sipp Mud Dep. | 208.2±54.2 | | 35.5±15.2 | |
| | Nobska Dep. | 348.0±35.3 | | 31.2±7.8 | |
| | Sipp Mud Flush | 236.5±35.2 | | 29.5±18.5 | |
| | Nobska Flush | 338.5±166.2 | | 28.5±17.6 | |

MAIN ARRAY EXPERIMENTS

Mean values of larval settlement for all Capitella sp. I experiments are given in Table III. The ANOVA for larvae in Capitella Main Array experiments indicated highly significant Batch (Flow), Column, Treatment, Flow x Treatment and Batch (Flow) x Treatment effects (Table VI). Given the batch-to-batch variation in larval recovery (Table III) and the many factors that may have contributed to it, the highly significant Batch (Flow) effect was not unexpected. An assumption for this analysis is that differences in number of larvae added did not cause the Batch variability, and given that the correlation between number of larvae added and number recovered was extremely weak, this assumption seems valid. The highly significant Batch (Flow) x Treatment effect may also have resulted from batch-to-batch variation in recovery; however, it also indicated that Treatment effects had to be analyzed separately for each experiment.

Tukey's tests revealed a fairly consistent pattern among the replicate experiments. For flow experiments (Fig. 4), settlement in NBH Mud Depressions did not differ significantly from Flush NBH Mud. Furthermore, with the exception of Capitella Flow 1, settlement in NBH Mud treatments was significantly greater than in either of the Glass Beads treatments. In Capitella Flow 1, the two mud treatments did not differ; however, Glass Beads Depressions did not differ from either Flush NBH Mud or NBH Mud Depressions. Except for Capitella Flow 1, significantly higher settlement was observed in Glass Beads Depressions compared with Flush Glass Beads in all flow experiments. In Capitella Still 1 and 3, enhanced settlement in depressions was not as apparent in that both mud treatments differed from both glass bead treatments, but

TABLE VI

ANOVA results for larvae in Capitella Main Array experiments and results of Tukey's tests for the significant column effect. Column 1 is closest to the outer flume wall. Data were log (x+1) transformed to homogenize variances.

| Source | df | SS | F | p |
|---|---|---|---|---|
| Flow | 1 | 10.053 | 3.839 | 0.107 |
| Batch (Flow) | 5 | 13.094 | 10.963 | 0.000*** |
| Treatment | 3 | 158.60 | 1.914 | 0.000*** |
| Row | 3 | 1.681 | 13.331 | 0.171 |
| Column | 3 | 8.422 | 50.516 | 0.000*** |
| Flow x Treatment | 3 | 12.598 | 4.013 | 0.028* |
| Flow x Row | 3 | 0.780 | 0.888 | 0.470 |
| Flow x Column | 3 | 0.515 | 0.816 | 0.505 |
| Batch (Flow) x Treatment | 15 | 15.698 | 4.381 | 0.000*** |
| Batch (Flow) x Row | 15 | 4.392 | 1.226 | 0.292 |
| Batch (Flow) x Column | 15 | 3.159 | 0.882 | 0.588 |
| Error | 42 | 10.033 | | |

*$p \leq 0.05$, ***$p \leq 0.001$

| Tukey's test | | | | |
|---|---|---|---|---|
| Column | 1 | 2 | 3 | 4 |
| Mean | 27.6 | 42.3 | 55.6 | 73.8 |

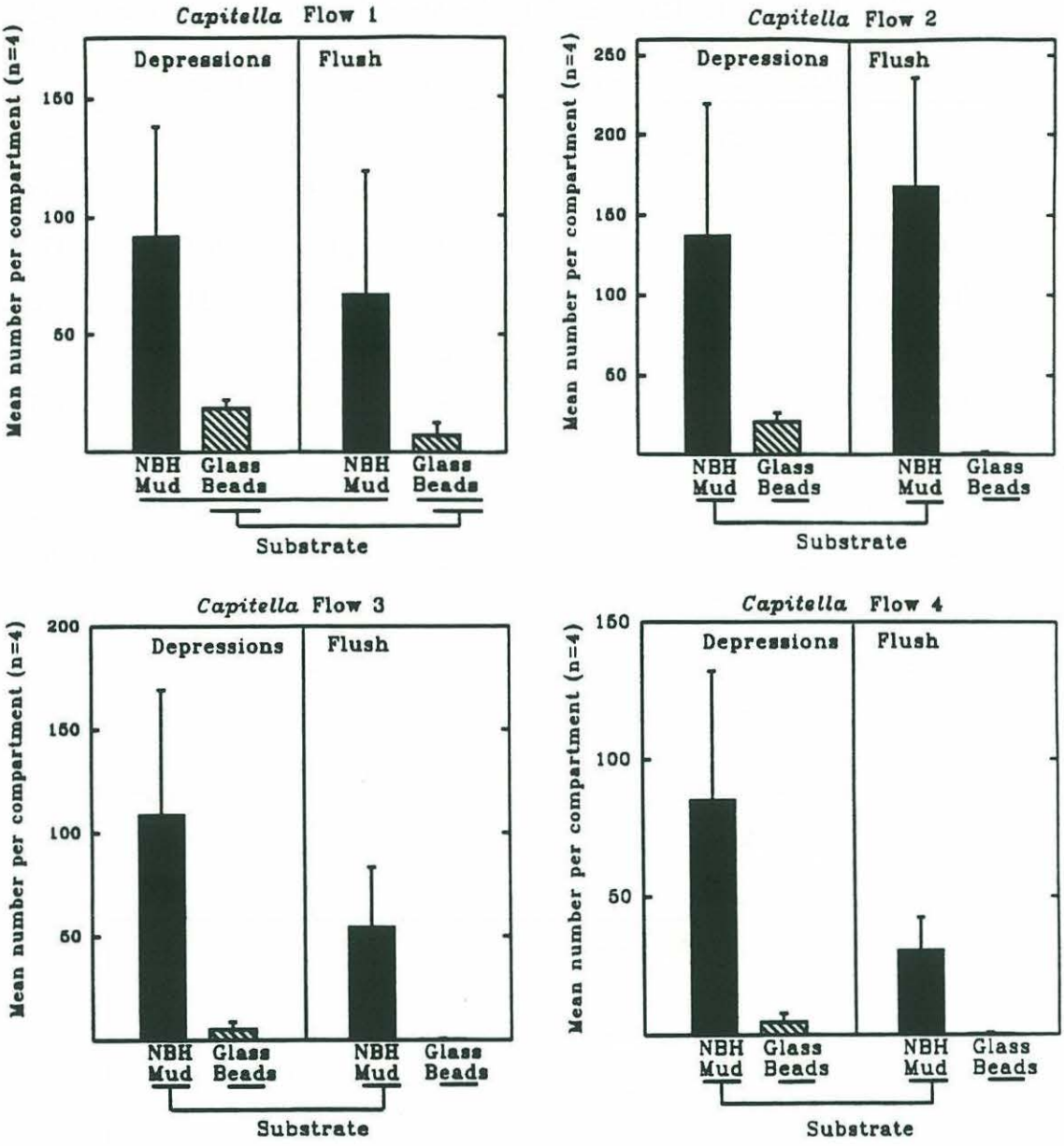


Figure 4. Results of Capitella Main Array, flow experiments. Vertical bars denote mean values, lines above them denote 1 standard deviation, and horizontal lines under each bar chart join treatments that were not significantly different as determined by a Tukey's Multiple Comparisons Test. Depressions are shown on left side of each bar chart and flush treatments on right.

neither sediment treatment had significantly higher settlement in depressions compared with flush treatments of the same sediment type (Fig. 5). Results of Capitella Still 2 suggest enhanced settlement in Glass Beads Depressions since densities differed from those in Flush Glass Beads but not from those in either of the NBH Mud treatments. The ambiguity of the depression enhancement effect in still-water experiments was probably the main contributor to the highly significant Flow x Treatment interaction in the overall ANOVA.

Because the Batch x Column interaction was not significant in the Capitella Main Array ANOVA, the significant Column effect was tested using Tukey's multiple comparisons of within-experiment column averages across all experiments (Table VI). Significantly higher settlement was observed in the column closest to the inner wall of the flume compared with the column closest to the outermost wall.

Statistical analysis of larval settlement in the Mulinia Main Array Experiments indicated similar significant effects as those for Capitella sp. I in that Batch (Flow), Treatment, and Batch (Flow) x Treatment effects were all highly significant (Table VII). In contrast to the Capitella experiments, however, Column and Flow x Treatment effects were not significant. Batch-to-batch variation in larval recovery (Table V) probably contributed to the highly significant Batch (Flow) and Batch (Flow) x Treatment effects. Because of this interaction, Treatment effect was analyzed separately for each experiment. Although trends in different experiments were similar, significant differences among treatments were not consistent. Settlement in NBH Mud Depressions was significantly higher than in all other treatments in Mulinia Flow 2, significantly

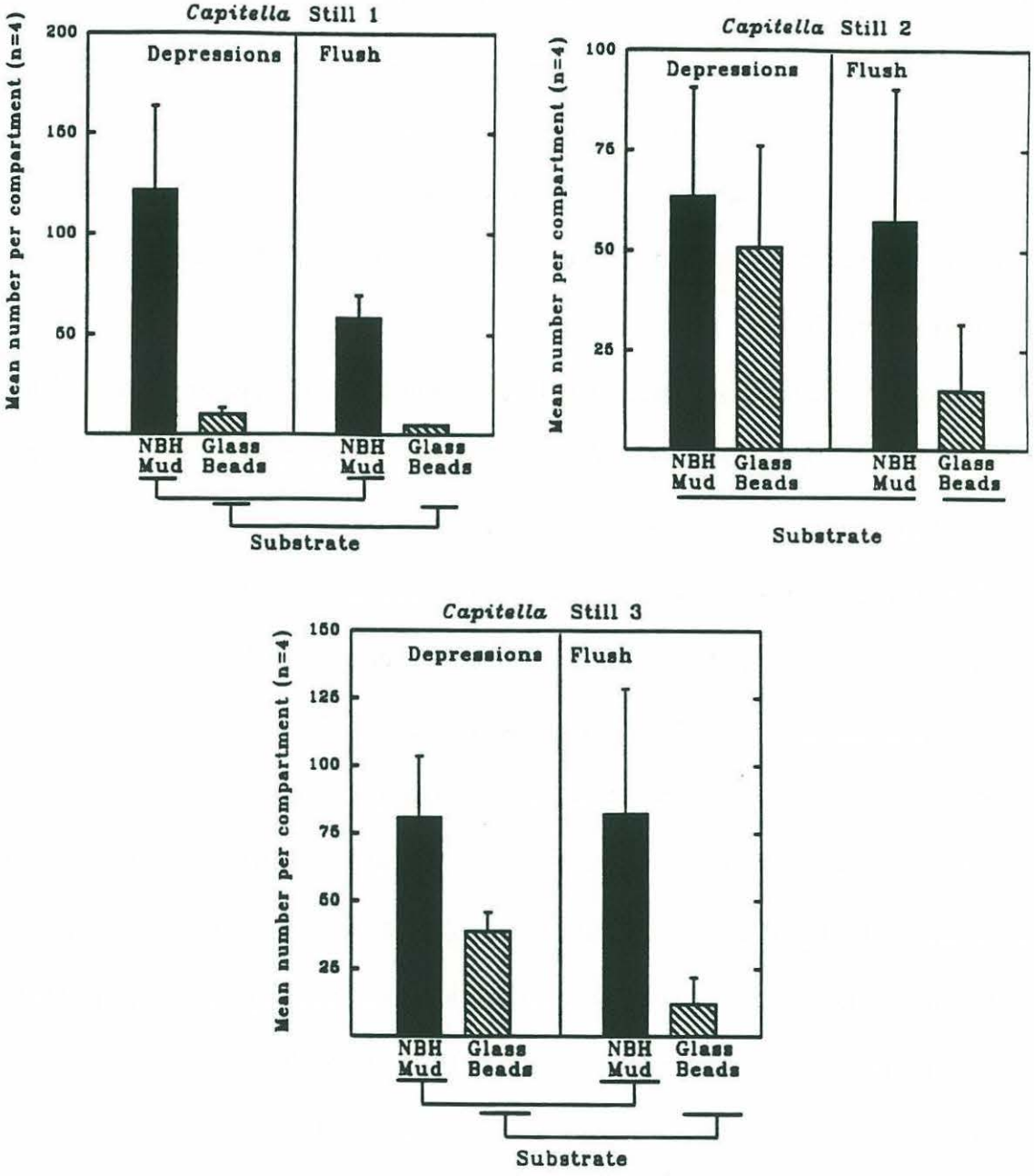


Figure 5. Results of Capitella Main Array, still-water experiments. See caption of Fig. 4 for explanation.

TABLE VII

ANOVA results for larvae in Mulinia Main Array experiments. Data were log (x+1) transformed to homogenize variances. Mulinia Flow 4 was analyzed separately because algae were added.

| Source | df | SS | F | p |
|---|---|---|---|---|
| Flow | 1 | 1.502 | 0.338 | 0.592 |
| Batch (Flow) | 2 | 17.803 | 21.802 | 0.000*** |
| Treatment | 3 | 86.904 | 20.378 | 0.000*** |
| Row | 3 | 0.107 | 0.172 | 0.913 |
| Column | 3 | 0.210 | 0.313 | 0.816 |
| Flow x Treatment | 3 | 10.748 | 2.52 | 0.107 |
| Flow x Row | 3 | 0.246 | 0.397 | 0.758 |
| Flow x Column | 3 | 2.196 | 3.277 | 0.059 |
| Batch (Flow) x Treatment | 12 | 17.059 | 6.693 | 0.000*** |
| Batch (Flow) x Row | 12 | 2.486 | 1.015 | 0.456 |
| Batch (Flow) x Column | 12 | 2.680 | 1.094 | 0.394 |
| Error | 36 | 7.349 | | |
| **Mulinia Flow 4** | | | | |
| Treatment | 3 | 25.946 | 50.832 | 0.000*** |
| Row | 3 | 0.526 | 1.031 | 0.443 |
| Column | 3 | 0.946 | 1.854 | 0.238 |
| Error | 6 | 1.020 | | |

***$p \leq 0.001$, *$p \leq 0.05$

higher than Flush NBH Mud and Flush Glass Beads in Flow 1, and significantly higher than only Flush Glass Beads in Flow 3 (Fig. 6). Glass Beads Depressions consistently had the second highest densities in all flow experiments; however, settlement was significantly higher than Flush NBH Mud only in Flow 1. Settlement in Glass Beads Depressions and Flush NBH Mud was significantly higher than Flush Glass Beads in all cases.

In Mulinia Flow 4, which was analyzed separately because of the potentially confounding factor of food addition, significantly higher settlement was observed in NBH Mud Depressions than in all other treatments (Fig. 6). Glass Beads Depressions and Flush NBH Mud were not significantly different, but both had significantly higher settlement than Flush Glass Beads. Thus, settlement patterns were very similar to those observed in experiments without food addition.

In Mulinia Main Array, still-water experiments, consistently higher settlement was observed in depressions than in the flush treatments (Fig. 7). In Still 2 and Still 3, but not Still 1, settlement in the two depression treatments did not differ significantly from one another. In Still 1 and Still 2, but not in Still 3, settlement in Flush NBH Mud and Flush Glass Beads was significantly different.

The spheres added with Capitella sp. I larvae showed no significant main effects and interaction terms in still-water experiments (Table VIII). Recovery of spheres in flow was too low for analysis. In flow and still-water experiments, however, mean densities in depressions tended to be higher than in flush treatments (Table III).

Results for spheres added with Mulinia lateralis larvae were very similar to those

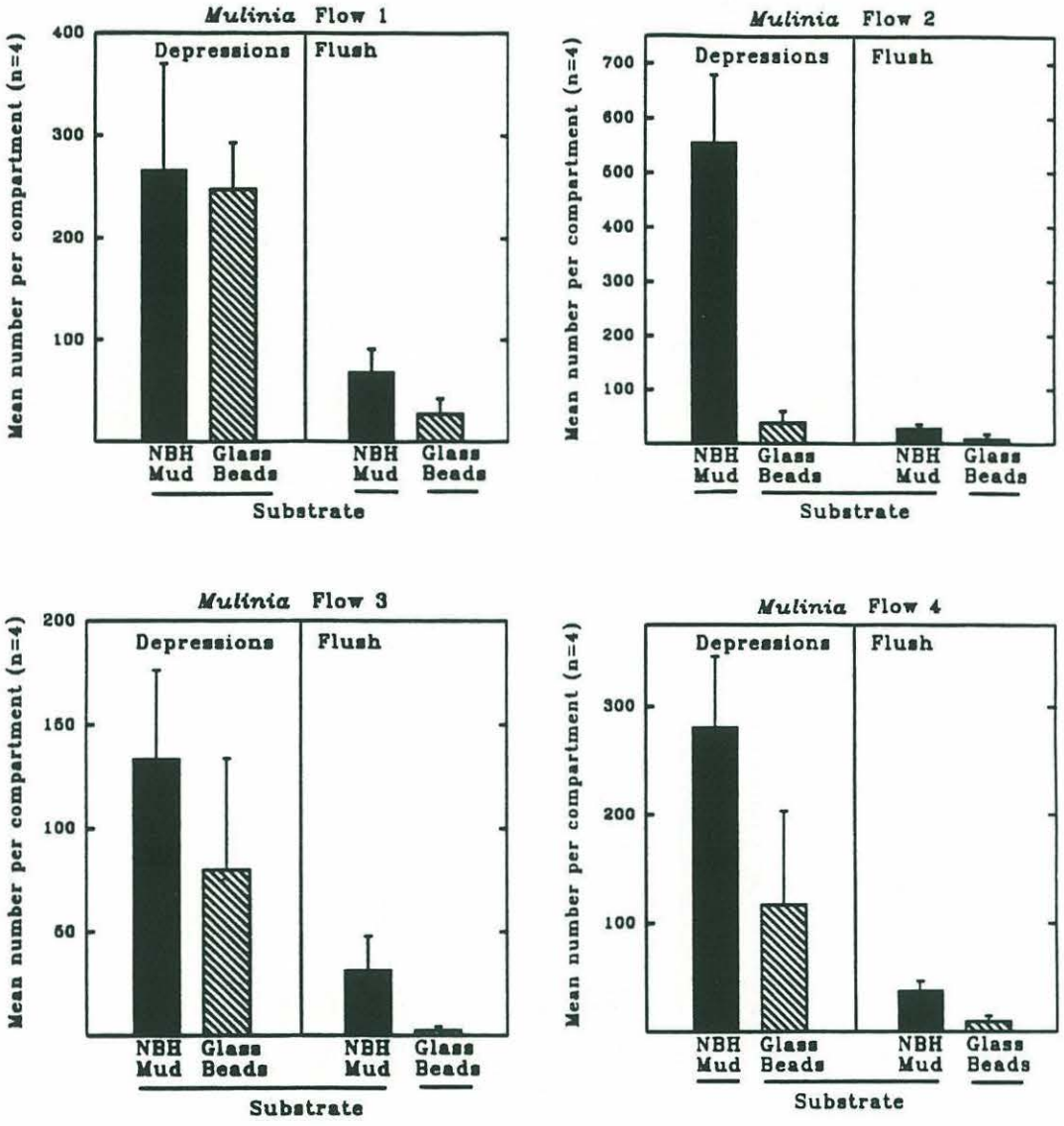


Figure 6. (A) Results of Mulinia Main Array, flow experiments. See caption of Fig. 4 for explanation.

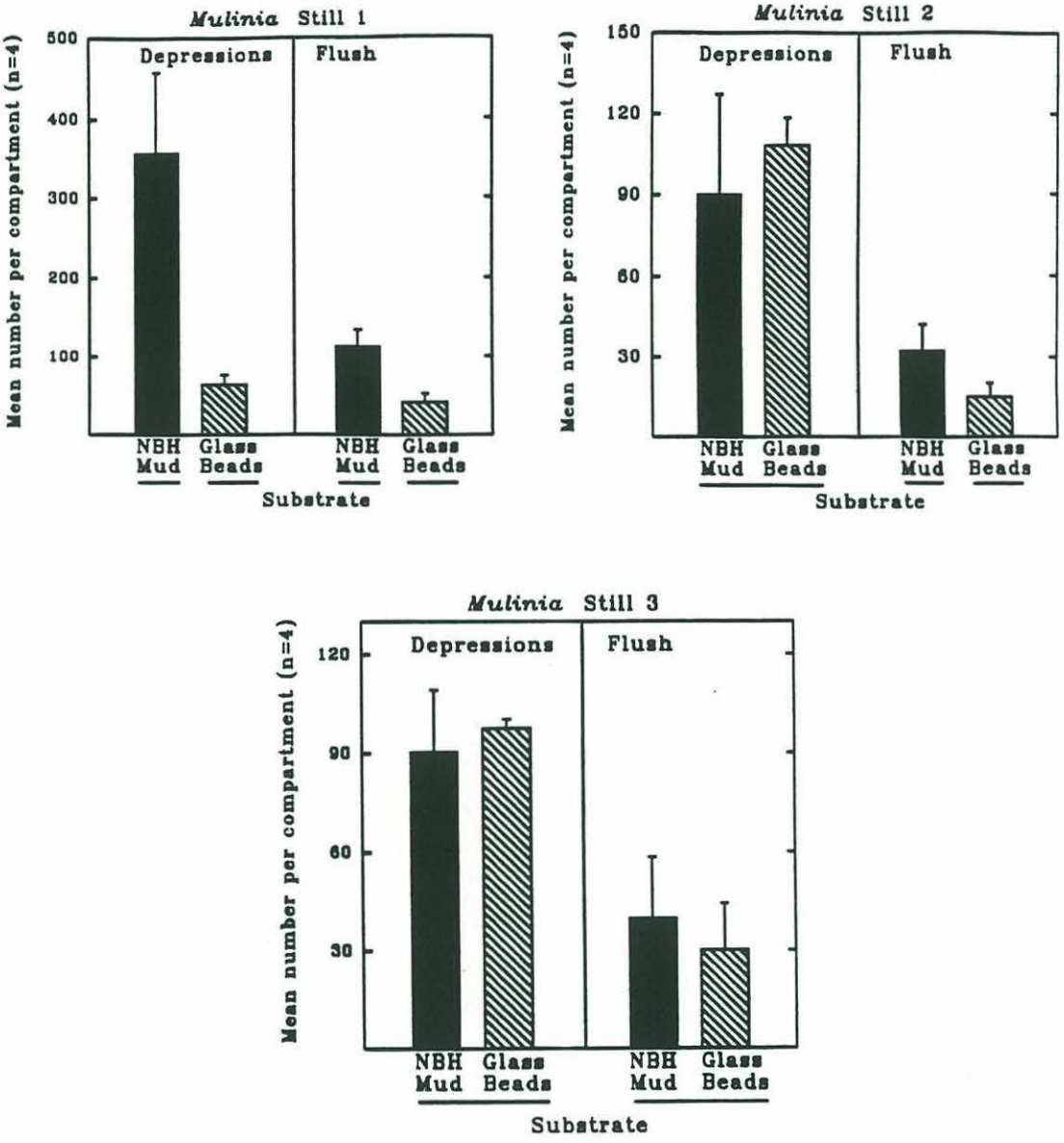


Figure 7. Results of Mulinia Main Array, still-water experiments. See caption of Fig. 4 for explanation.

TABLE VIII

ANOVA results for spheres in Capitella Main Array still-water experiments.

| Source | df | SS | F | p |
|---|---|---|---|---|
| Batch | 2 | 45.50 | 0.885 | 0.430 |
| Treatment | 3 | 244.92 | 4.088 | 0.067 |
| Row | 3 | 50.25 | 1.331 | 0.349 |
| Column | 3 | 48.92 | 2.232 | 0.185 |
| Batch x Treatment | 6 | 119.83 | 0.777 | 0.598 |
| Batch x Row | 6 | 75.50 | 0.490 | 0.808 |
| Batch x Column | 6 | 43.83 | 0.284 | 0.937 |
| Error | 18 | 462.50 | | |

*$p \leq 0.05$

added with Capitella sp. I larvae. Although significant Treatment and Batch x Row effects were observed in still-water experiments (Table IX), across-experiment Tukey's comparisons of within-experiment Treatment averages failed to reveal any significant differences. In flow experiments, no significant main effects and interaction terms were observed for spheres in Mulinia Flow 2 and a significant treatment effect was observed for spheres in Mulinia Flow 4. A Tukey's test indicated significantly higher numbers of spheres in Glass Beads Depressions compared with Flush NBH Mud and Flush Glass Beads. Sphere recovery was too low in other experiments for analysis, though densities in depressions tended to be slightly higher than those in flush treatments (Table V).

SMALL ARRAY EXPERIMENTS

Analysis of variance for the Capitella Small Array experiments indicated a significant Treatment effect for larvae in flow and still-water experiments (Table X) but no significant depression effect (Fig. 8). In flow and still-water experiments, Tukey's tests indicated significantly higher settlement in NBH Mud Depressions and Flush NBH Mud compared with Glass Beads Depressions and Flush Glass Beads (Fig. 8). NBH Mud Depressions did not significantly differ from Flush NBH Mud and Glass Beads Depressions did not differ from Flush Glass Beads.

In the Mulinia Small Array experiments, a highly significant Treatment effect was observed for larvae in Flow A, Flow B, and Still A (Table XI). In Still B, none of the effects were significant. As in the Mulinia Main Array experiments, Tukey's tests indicated different treatment effects. In Flow A, significantly more larvae were found

TABLE IX

ANOVA results for spheres in Mulinia Main Array experiments and results of Tukey's tests for the significant Treatment effects. Mulinia Flow 2 data were log (x+1) transformed to homogenize variances.

| Source | df | SS | F | p |
|---|---|---|---|---|
| **Still Water Experiments** | | | | |
| Batch | 2 | 10.292 | 0.942 | 0.408 |
| Treatment | 3 | 98.229 | 6.196 | 0.029* |
| Row | 3 | 19.896 | 0.296 | 0.828 |
| Column | 3 | 33.563 | 1.094 | 0.421 |
| Batch x Treatment | 6 | 31.708 | 0.967 | 0.475 |
| Batch x Row | 6 | 134.54 | 4.103 | 0.009*** |
| Batch x Column | 6 | 61.375 | 1.872 | 0.141 |
| Error | 18 | 98.375 | | |
| **Mulinia Flow 2** | | | | |
| Treatment | 3 | 1.118 | 0.343 | 0.796 |
| Row | 3 | 1.871 | 0.573 | 0.653 |
| Column | 3 | 1.279 | 0.392 | 0.764 |
| Error | 6 | 6.528 | | |
| **Mulinia Flow 4** | | | | |
| Treatment | 3 | 604.25 | 16.01 | 0.003** |
| Row | 3 | 24.75 | 0.656 | 0.608 |
| Column | 3 | 61.25 | 1.623 | 0.281 |
| Error | 6 | | | |

*$p \leq 0.05$, **$p \leq 0.01$, ***$p \leq 0.001$

TABLE IX (cont.)
ANOVA results for spheres in Mulinia Main Array experiments and results of Tukey's tests for the significant Treatment effects. Mulinia Flow 2 data were log (x+1) transformed to homogenize variances.

| Tukey's test | **Combined Still Water** | | | |
|---|---|---|---|---|
| Treatment | NBH Dep | GB Dep | NBH Flush | GB Flush |
| Mean | 6.25 | 5.58 | 3.42 | 2.83 |

| | **Mulinia Flow 4** | | | |
|---|---|---|---|---|
| Treatment | GB Dep | NBH Dep | NBH Flush | GB Flush |
| Mean | 18.25 | 10.5 | 3.25 | 3.50 |

| | | | | |
|---|---|---|---|---|
| Mean | | | | |

TABLE X
ANOVA results for Capitella Small Array experiments.

| | | Larvae | | | Spheres | |
|---|---|---|---|---|---|---|
| Source | df | SS | F | p | SS | F | p |
| **Flow** | | | | | | |
| Row | 3 | 2.00 | 1.37 | 0.340 | Spheres not added for this experiment | |
| Column | 3 | 4.79 | 3.27 | 0.101 | | |
| Treatment | 3 | 27.19 | 18.56 | 0.002** | | |
| Error | 6 | 2.93 | | | | |
| **Still** | | | | | | |
| Row | 3 | 1.03 | 1.74 | 0.257 | 149.69 | 0.56 | 0.661 |
| Column | 3 | 0.36 | 0.62 | 0.629 | 130.19 | 0.49 | 0.704 |
| Treatment | 3 | 27.50 | 46.73 | 0.000*** | 657.69 | 2.46 | 0.160 |
| Error | 6 | 1.18 | | | 534.34 | | |

***$p \leq 0.001$, **$p \leq 0.01$

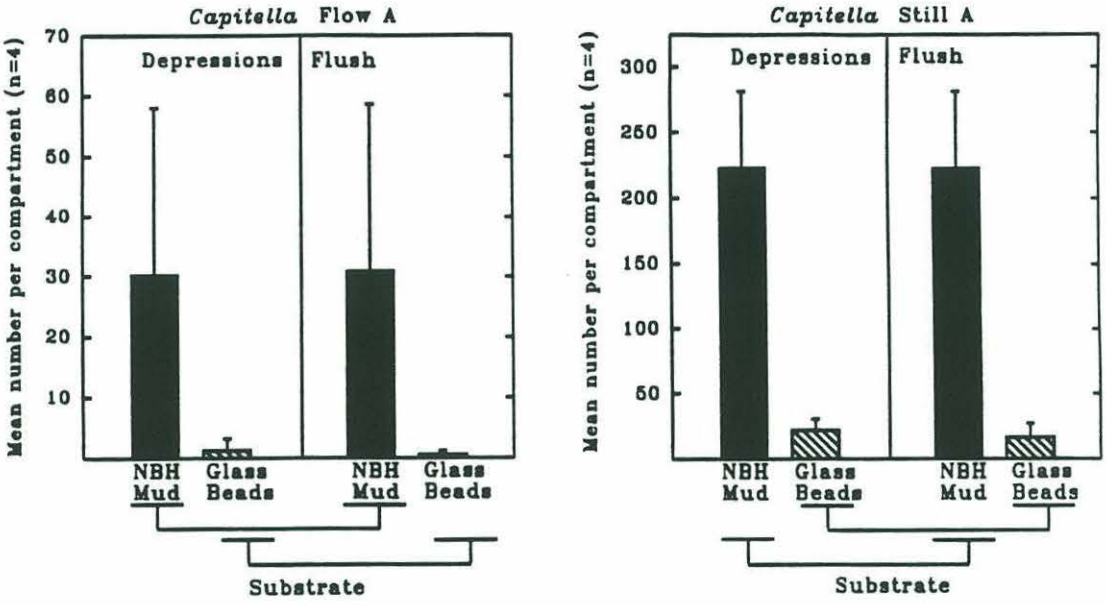


Figure 8. Results of Capitella Small Array, flow experiment and Capitella Small Array, still-water experiment. See caption of Fig. 4 for explanation.

TABLE XI

ANOVA results for Mulinia Small Array experiments and results of Tukey's tests for the significant Column and Row effects. Row 1 was at the leading (upstream) edge of the array and Column 1 was closest to the outer flume wall. Data for larvae in Flow B and Still B were log (x+1) transformed to homogenize variances.

| | | Larvae | | | Spheres | | |
|---|---|---|---|---|---|---|---|
| Source | df | SS | F | p | SS | F | p |
| **Flow A** | | | | | | | |
| Treatment | 3 | 1261.2 | 33.24 | 0.000*** | | | |
| Row | 3 | 109.69 | 2.89 | 0.124 | | Not Applicable | |
| Column | 3 | 24.19 | 0.64 | 0.168 | | | |
| Error | 6 | 75.88 | | | | | |
| **Flow B** | | | | | | | |
| Treatment | 3 | 2.60 | 11.27 | 0.007*** | 16.19 | 1.59 | 0.288 |
| Row | 3 | 0.57 | 2.47 | 0.159 | 48.69 | 4.78 | 0.050* |
| Column | 3 | 1.37 | 5.95 | 0.031* | 23.19 | 2.28 | 0.180 |
| Error | 6 | 0.46 | | | 20.375 | | |
| **Still A** | | | | | | | |
| Treatment | 3 | 45121.2 | 12.78 | 0.005** | 114.75 | 0.476 | 0.710 |
| Row | 3 | 1953.2 | 0.25 | 0.860 | 140.75 | 0.584 | 0.647 |
| Column | 3 | 12118.2 | 2.18 | 0.191 | 2.25 | 0.009 | 0.999 |
| Error | 6 | 7849.38 | | | 482.00 | | |

TABLE XI (cont.)

ANOVA results for Mulinia Small Array experiments and results of Tukey's tests for the significant Column and Row effects. Row 1 was at the leading (upstream) edge of the array and Column 1 was closest to the outer flume wall. Data for larvae in Flow B and Still B were log (x+1) transformed to homogenize variances.

| Tukey's test | **Flow B Larvae Column** | | | |
|---|---|---|---|---|
| Column | 1 | 2 | 3 | 4 |
| Mean | 12.5 | 15.0 | 18.0 | 30.0 |

| | **Flow B Spheres Row** | | | |
|---|---|---|---|---|
| Row | 1 | 2 | 3 | 4 |
| Mean | 5.5 | 3.0 | 2.0 | 0.75 |

TABLE XI (cont.)

ANOVA results for Mulinia Small Array experiments and results of Tukey's tests for the significant Column and Row effects. Row 1 was at the leading (upstream) edge of the array and Column 1 was closest to the outer flume wall. Data for larvae in Flow B and Still B were log (x+1) transformed to homogenize variances.

| | | Larvae | | | Spheres | | |
|---|---|---|---|---|---|---|---|
| Source | df | SS | F | p | SS | F | p |
| **Still B** | | | | | | | |
| Treatment | 3 | 0.71 | 2.93 | 0.12 | 114.69 | 0.25 | 0.861 |
| Row | 3 | 0.12 | 0.51 | 0.69 | 121.69 | 0.26 | 0.850 |
| Column | 3 | 0.41 | 1.69 | 0.27 | 1776.2 | 3.83 | 0.076 |
| Error | 6 | 0.48 | | | 927.88 | | |

$^{***}p \leq 0.001$, $^{**}p \leq 0.01$, $^{*}p \leq 0.05$

in Nobska Sand Depressions and significantly fewer larvae were found in Flush Sipp Mud compared with other treatments (Fig. 9). This suggests a depression effect in flow. In Flow B, however, both Nobska Sand Treatments were significantly higher than both Sipp Mud treatments, but neither of the Depression/Flush contrasts differed when sediment type was the same. Thus, no depression effect was observed in Flow B. In the still-water experiments (Fig. 10), larvae were either non-selective (Still B), or showed a very weak depression enhancement (Still A). In Still A, significantly higher numbers of larvae were observed in Sipp Mud Depressions compared to Flush Sipp Mud, and Flush Sipp Mud had significantly lower settlement than either of the Nobska Sand treatments. No settlement enhancement was observed in Nobska Sand Depressions compared with Flush Nobska Sand. The most surprising result of these experiments, however, was the clear preference for a low-organic sediment (Nobska Sand) over an organic-rich sediment (Sipp Mud). This was unexpected given the results of the NBH Mud/Glass Beads experiments in the Main Array.

A significant Column effect was observed for Mulinia lateralis larvae in Flow B (Table XI), and a Tukey's test indicated significantly higher numbers in the innermost column compared with the outermost column. This result is similar to that for the Capitella Main Array experiment.

For spheres added in Capitella Still A, there were no significant main effects (Table X). Spheres were not added in Capitella Flow A. Spheres added with Mulinia lateralis larvae showed a weakly significant Row effect in Flow B (Table XI). Tukey's test indicated significantly higher sphere recovery in the furthest row upstream compared

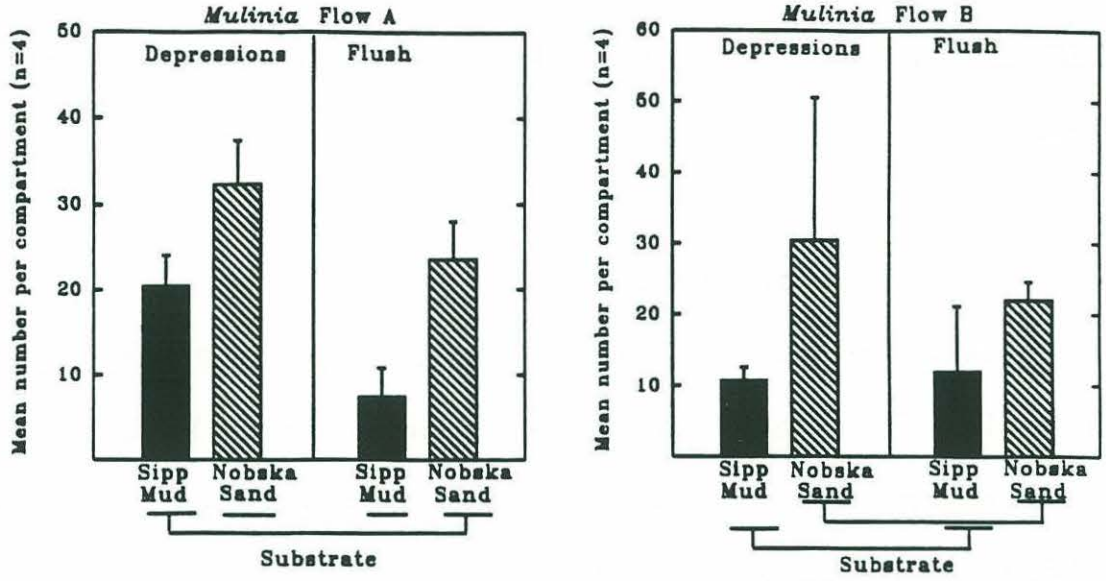


Figure 9. Results of Mulinia Small Array flow experiments. See caption of Fig. 4 for explanation.

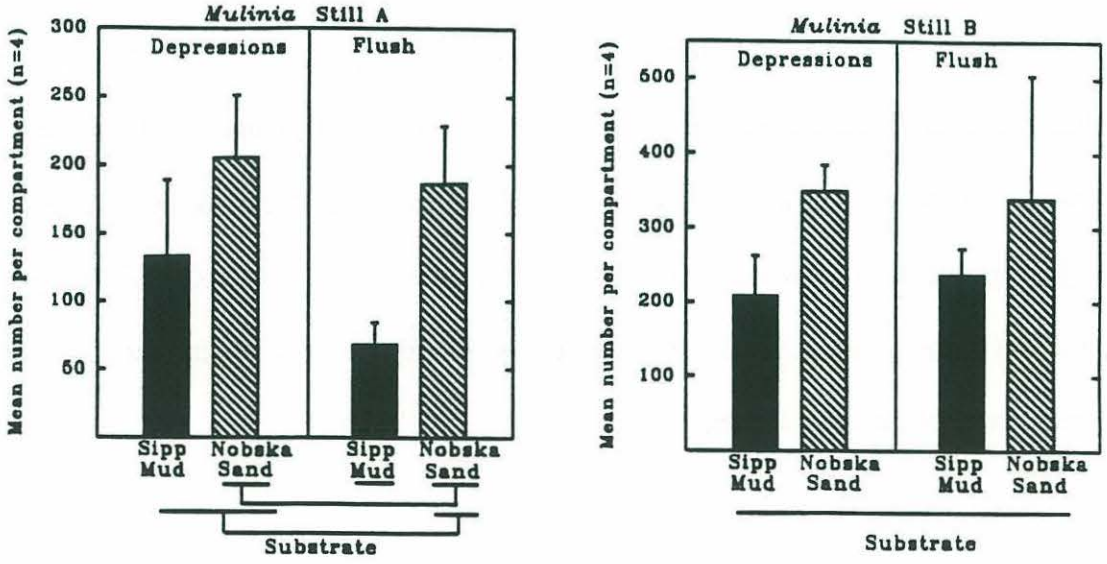


Figure 10. Results of Mulinia Small Array still-water experiments. See caption of Fig. 4 for explanation.

with that in the furthest row downstream, but none of the other rows were significantly different. Recovery of spheres in Mulinia Flow A was too low for meaningful statistical tests.

SWIMMERS VS. SETTLERS

The high number of Capitella sp. I larvae in the Glass Beads Depressions may, in part, have been the result of temporary entrainment of swimming larvae that had not metamorphosed (Table XII). A comparison of swimming larvae and metamorphosed Capitella sp. I juveniles in Flow 2 (Table XII) indicated that the majority of swimming larvae were found in Glass Beads Depressions. Numbers of swimming larvae in other experiments were usually lower; however, this particular example illustrates that swimming larvae likely explain, at least in part, enhanced numbers of Capitella sp. I larvae in an undesirable sediment (Glass Beads Depressions).

For Mulinia lateralis, comparable numbers of swimmers were observed in NBH Mud and Glass Bead Depressions (Table XIII). This may be explained by settlement behavior of M. lateralis larvae; even in the presence of a suitable sediment, settlement of M. lateralis larvae is not rapid (Snelgrove, pers. obs.). Numbers of swimmers observed in depressions, however, were clearly insufficient to qualitatively explain the depression enhancement effect.

TABLE XII

Proportion of swimming larvae observed in each treatment immediately after the sediments were removed from Capitella Flow 2.

| Treatment | Number of Replicates | Number of Swimmers ($\bar{x}$±1sd) | Number Recovered ($\bar{x}$±1sd) | Percent Swimmers ($\bar{x}$±1sd) |
|---|---|---|---|---|
| NBH Depression | 4 | 0.2±0.5 | 137.0±82.5 | 0.2±0.4 |
| GB Depression | 4 | 14.5±6.8 | 20.8±5.7 | 66.8±21.5 |
| NBH Flush | 4 | 0.0±0.0 | 167.5±69.2 | 0.0±0.0 |
| GB Flush | 4 | 0.0±0.0 | 0.8±1.0 | 0.0±0.0 |

TABLE XIII

Proportion of swimming larvae observed in each treatment immediately after the sediments were removed from Mulinia Still 2. Not all replicate compartments were examined because of time constraints.

| Treatment | Number of Replicates | Number of Swimmers ($\bar{x}$±1sd) | Number Recovered ($\bar{x}$±1sd) | Percent Swimmers ($\bar{x}$±1sd) |
|---|---|---|---|---|
| NBH Mud Depression | 4 | 7.8±3.8 | 90.0±37.3 | 8.8±4.4 |
| GB Depression | 4 | 12.2±7.1 | 108.0±10.3 | 11.7±7.5 |
| Flush NBH Mud | 2 | 0.5±0.7 | 25.0±5.7 | 1.7±2.4 |
| Flush GB | 2 | 0.0±0.0 | 10.5±0.7 | 0.0±0.0 |

# DISCUSSION

## LARVAL SELECTIVITY

Larvae of Capitella sp. I and Mulinia lateralis clearly are capable of active sediment selection, with both species settling in higher numbers in NBH Mud than in Glass Beads when treatments were flush with the flume bottom. This is consistent with previous results for these species (Butman et al., 1988b; Grassle et al., 1992; Butman & Grassle, in press; Grassle et al., in press). In terms of sediment choices, the most surprising result of our experiments was that, contrary to all other choice experiments, where high organic NBH Mud was chosen over low organic Glass Beads, M. lateralis larvae generally selected low organic Nobska Sand over the organically rich Sipp Mud (Figs. 9,10) in small array experiments. Mulinia lateralis is not known to occur in the area where Sippewissett Mud was collected, despite the high organic content of this sediment. We can only speculate as to what may have resulted in active selection for Nobska Sand or rejection of Sipp Mud. Sipp Mud, for example, may have contained chemical compounds that repelled M. lateralis larvae (e.g., Woodin, 1991) or lacked chemical compounds that may attract the larvae. Other factors, such as differences in grain-size distribution between the NBH Mud and Sipp Mud, may also have been responsible.

The goal of these experiments is to weigh the relative importance of active behavior versus hydrodynamic processes in determining small-scale distributions of larvae. To make this assessment, near-bed hydrodynamics were manipulated (i.e.,

sediment depressions) in a way that was expected to alter distributions of passive larval mimics. Unfortunately, the passive larval mimics used in this study were rarely collected in sufficient numbers to make this comparison adequately. Insight regarding the passive hydrodynamic trapping characteristics of the depressions can, however, be gleaned from the literature and is provided in the section that follows. Thus, theoretical arguments are used to describe qualitatively how the hydrodynamics associated with depressions result in passive particle collection, allowing us to test the passive deposition hypothesis for settling larvae.

## HYDRODYNAMIC TRAPPING CHARACTERISTICS OF DEPRESSIONS

Flow visualizations and models (O'Brien, 1972; Brandeis, 1982; Sinha et al., 1982; Takematsu, 1966; Taneda, 1979; Weiss & Florsheim, 1965), as well as dimensional analysis (Butman et al., 1986) indicate that trapping efficiency of depressions is determined by aspect ratio ($H$ / $D$, where $H$ is depression height and $D$ is diameter), depression Reynolds number ($R_t = u_f D / \nu$, where $u_f$ is mean horizontal velocity at the pit opening and $\nu$ is the fluid kinematic viscosity), $u_f / W$, where $W$ is particle fall velocity, $W d / \nu$, where $d$ is particle diameter, $\rho_p / \rho_f$, where $\rho_p$ is particle density and $\rho_f$ is fluid density, and $N_c d^3$, where $N_c$ is number of particles in the fluid. Thus, depression geometry, bottom flow conditions and particle characteristics all contribute to how depressions trap passive particles.

Two-dimensional flow over depression-like cavities has been well documented, and although flow in shallow cavities is complicated (e.g., Sinha et al., 1982), the flow

in and around cavities with aspect ratios approaching one appears relatively simple (e.g., Pan & Acrivos, 1967; Taneda, 1979). The boundary layer detaches at the upstream edge of the cavity, largely bypasses the cavity itself and then reattaches at the downstream edge. Inside the cavity, a single recirculating eddy forms unless the aspect ratio of the cavity is significantly higher than unity, in which case several vertically stacked recirculating eddies may form. These conclusions have been drawn from flow visualization experiments (Weiss & Florsheim, 1965) and numerical models (Pan & Acrivos, 1967), and appear to be consistent over cavity Reynolds numbers ranging from $R_t << 1$ (Pan & Acrivos, 1967) to $R_t \approx 2 \times 10^5$ (Haugen & Dhanak, 1966). Although three-dimensional flow is more complicated and poorly known, the flow at relatively low $R_t$ should be comparable to the two-dimensional case over at least the central portion of the cavity (Koseff & Street, 1984). Furthermore, the flow along the dominant flow vector in conical depressions appears to be at least grossly comparable to that in rectangular cavities (Yager et al., submitted).

Unfortunately, little direct information exists on precisely how particles accumulate in depressions within the sediment bed, and conclusions must be inferred from sediment trap studies. Sediment trap studies offer predictive value from both theoretical (Butman et al., 1986) and experimental (e.g., Hargrave & Burns, 1979; Gardner, 1980; Butman, 1986b) results. As the aspect ratio of a trap increases, so does collection efficiency because particle residence time increases and probability of resuspension decreases. An increase in $u_f / W$ or $R_t$ will reduce trapping efficiency because of increased resuspension. Because $R_t$ is proportional to both trap diameter and

mean flow speed at the trap mouth, higher $R_t$ results in decreased particle trapping, particularly for light particles. This explains why light particles are known to accumulate in depressions under some conditions (e.g., Risk & Craig, 1976), and heavy particles accumulate under others (e.g., Nelson et al., 1987).

Although relative enhancement of vertical fluid shear compared to flush sediment may be observed along the central areas of the walls of a depression (Roshko, 1955), areas in the corners of depressions are relatively stagnant and will tend to accumulate particles. Light particles enter depressions as a result of flow exchange at the downstream edge of the depression where pulses of water enter; mass balance requires that a corresponding loss of water must occur at the upstream edge (Rockwell & Naudascher, 1978). This provides the mechanism for entrainment and accumulation of light particles in particular, which, in sediment trap studies, appear to enter via this mechanism rather than by direct settlement (e.g., Hargrave & Burns, 1979; Butman, 1986b).

Sediment trap theory suggests that as $R_t$ increases or aspect ratio decreases, particle trapping efficiency (amount of material collected per unit mouth area) should decrease (Butman et al., 1986). Thus, in these experiments, the expectation is that a depression enhancement effect would be at least as strong for passive particles in the small versus the large depressions, given the higher aspect ratio and lower trap Reynolds number in the small depressions.

## SPHERE ENTRAINMENT AND RETENTION IN DEPRESSIONS

Although particles may be transported into depressions (i.e., entrained), this does not ensure that they will necessarily be retained (i.e., deposited and not resuspended). Based on the literature, the hydrodynamic regime in the depressions in our experiments should have entrained passive particles. We can only infer, however, that entrainment of particles would result in retention within the depressions under these flume flow conditions because existing sediment trap studies (e.g., Lau, 1979; Butman, 1986b) employed higher aspect ratios or higher $R_t$ than those of our depressions. Extrapolation from these studies suggests that passive larval mimics carried into the depressions will not be resuspended in the flume flow. This is consistent with direct visual observations of particle behavior in the depressions, where no resuspension was noted (Snelgrove, pers. obs.). Furthermore, we have observed accumulation of light flocculent matter in very small depressions in the flume under comparable flow conditions and aspect ratio but where $R_t$ was much lower than in our experimental depressions.

Additional support for particle deposition in depressions in the flume flow comes from the elevated numbers of spheres collected in depressions compared with flush treatments. Differences were rarely significant (Table IX), and only in Mulinia Flow 4 were significantly more spheres recovered in a depression treatment ( $\bar{x}$ = 18.25 in Glass Beads Depressions) compared with flush treatments ( $\bar{x}$ = 3.25 in Flush NBH Mud and 3.50 in Flush Glass Beads). In all other cases, numbers of spheres were generally higher in depressions (Tables III, IV). In flow, the negatively buoyant spheres passed over the array once only, allowing just one opportunity for entrainment in depressions. This likely contributed to poor sphere (compared to larval) recovery in flow. Sphere

recovery has been much lower than larval recovery in sediment arrays in virtually all of our flume studies where 383-μm, polystyrene spheres were chosen as passive larval mimics (e.g. Butman et al., 1988b; Grassle & Butman, 1989; Grassle et al., 1992; Butman & Grassle, in press; Grassle et al., in press). In fact, the spheres may not be adequate passive larval mimics because they were selected to match only gravitational fall velocity of larvae (or downward swim speed in Capitella sp. I) and not larval size, and there is evidence (published after these experiments were conducted) that behavior of relatively large, low density particles in boundary-layer flow is a function of both $u_f$ / $W$ and particle Reynolds number (see discussion in Butman & Grassle, in press). Based on scaling arguments, however, larger spheres (e.g., 450-500 μm in diameter, to mimic settling Capitella sp. I larvae; Butman et al., 1988a) would also be expected to collect in higher numbers in depressions.

In summary, based on hydrodynamic scaling arguments and previous empirical studies, the depressions chosen for these flume experiments are expected to collect passive larval mimics in higher numbers than flush sediments in the flume flow. Collections of the mimics used here qualitatively support, but do not quantitatively test, this prediction.

## LARVAL ENTRAINMENT AND RETENTION IN DEPRESSIONS

A depression enhancement effect was more apparent for larvae than for spheres. Significantly higher densities of larvae were often observed in depressions for a given sediment treatment. Larvae are capable of upward swimming (e.g., Chia et al., 1984),

resulting in neutrally or slightly negatively buoyant particles that could recirculate in the flume. Larvae may be more likely to accumulate in depressions than the spheres because they make multiple passes over the array and thus have a greater probability of being entrained. Indeed, in flow experiments, significantly higher densities of Capitella sp. I and Mulinia lateralis larvae were observed in Glass Beads Depressions compared with Flush Glass Beads, and numbers in NBH Mud Depressions were generally (though not necessarily significantly) higher than in Flush NBH Mud. Thus, larval settlement in both species was enhanced in depressions, apparently as a result of hydrodynamic entrainment.

The major difference between the two species was that Capitella sp. I settled in higher numbers in NBH Mud than Glass Beads, regardless of whether treatments were flush or depressions, whereas Mulinia lateralis larvae were consistently more abundant in Glass Beads Depressions (a "poor choice") than in Flush NBH Mud (a "good choice"). These results suggest that larvae of both species are entrained in depressions, as illustrated by higher densities in depressions for a given treatment, but that Capitella sp. I larvae are capable of "escape" if the sediment is unsuitable.

Although numbers of spheres and larvae of both species tended to be higher in depressions for a given treatment in still-water experiments, significant differences were observed in only some instances. Higher numbers of spheres in depressions in still-water experiments (Tables III, V) may be explained by the greater likelihood of spheres rolling into and remaining in depressions than on flush sediment surfaces. In still water, we observed that Mulinia lateralis larvae tended to swim up in vertical spirals, close

their valves, and then sink quickly to the bottom, a behavior that has been observed for other bivalve larvae (e.g., Jonsson et al., 1991). This behavior may be repeated, even if a suitable substrate is present. If individuals, particularly older, competent pediveligers, sink into a depression, they may be unable to swim out. As larvae get older and heavier, their swimming ambit is reduced such that hydrodynamic trapping may increase with larval age (Snelgrove, pers. obs.). Decreasing swimming ability with increasing size may explain why significantly higher numbers of M. lateralis larvae were observed in depressions regardless of sediment type in some experiments but not others. This may also explain why, in the small-array experiments, depression enhancement was observed for M. lateralis in only one of the two flow and one of the two still-water experiments. Capitella sp. I larvae showed no significant depression effect in the small array, again suggesting that retention in depressions may be scale dependent. Thus, hydrodynamic trapping may be dependent on physiological age as well as the scale of the entrainment eddy.

Two other observations provide indirect evidence for hydrodynamic modification of settlement in Capitella sp. I. First, in Main Array flow experiments, high densities of pock marks on the surface of the fine sediment indicated that settlement of Capitella sp. I larvae was much more concentrated at the upstream edge of NBH Mud Depressions compared with a more dispersed distribution of pock marks in Flush NBH Mud. This presumably was the result of flow delivery to sediment in the depressions by the recirculating eddy. Second, higher densities of larvae were collected in the innermost, compared with the outermost, column in Capitella Main Array, flow

experiments (Table VI). This is likely a result of a weak, cross-stream circulation that occurs in any racetrack-design flume (e.g., Butman & Grassle, in press). In this secondary flow, particles or larvae circulating in water just above the bottom and that are sufficiently negatively buoyant may accumulate toward the inner wall of the flume over time. Capitella sp. I larvae appear to be particularly vulnerable to this type of transport because they swim so close to the bottom in still water (Butman et al., 1988a), unlike Mulinia lateralis which tend to move in vertical spirals. Although M. lateralis larvae also stay close to the bottom (Grassle et al., 1992), the vertical excursions may be sufficient to reduce a cross-stream flow effect. Cross-stream enhancement was observed for M. lateralis larvae in one of the small array experiments (Flow B), however, no effect was observed in Main Array, flow experiments (Table VII).

Entrainment in depressions does not ensure that larvae will settle and metamorphose. Unlike spheres, which should be retained under these flow conditions once they are entrained in depressions, larvae may choose not to settle and instead swim out of depressions. Some Capitella sp. I larvae that were present in Glass Beads Depressions may have been trapped only temporarily and did not metamorphose (Table XII), likely because Capitella sp. I larvae are capable of delaying metamorphosis in the absence of a suitable sediment (Pechenik & Cerulli, 1991). The low numbers of swimming Capitella sp. I larvae in NBH Mud treatments is undoubtedly the result of rapid settlement in a preferred substrate, as observed in competency tests conducted concurrently with these and other experiments (Butman et al., 1988b; Butman & Grassle, in press; Grassle et al., in press). In examining the sediment in Glass Beads Depressions

immediately after the completion of other experiments, we have often observed that fewer individuals had not settled and more individuals had metamorphosed (Snelgrove et al., unpublished data). We attribute this to tiny clumps of NBH Mud that occasionally contaminated Glass Beads Depressions during preparation of the array, providing enough cue to induce metamorphosis even in this unfavorable habitat. Relatively little sediment cue is necessary to induce settlement of Capitella sp. I larvae (Butman & Grassle, in press; Grassle et al., in press). Relatively few Mulinia lateralis larvae in depressions had failed to settle and metamorphose (Table XIII), and similar numbers of swimmers were observed in NBH Mud and Glass Beads Depressions.

## LARVAL RECOVERY IN THE SEDIMENT ARRAYS

That a higher proportion of Capitella sp. I than Mulinia lateralis larvae were recovered in the arrays is understandable, given that Capitella sp. I larvae respond more quickly and selectively in competency experiments. Development time and size were somewhat variable in M. lateralis larvae (Table IV), and may have contributed to the variability in results. Mean shell length was weakly, but not significantly, correlated with percentage larval recovery ($r = 0.681$, $p = 0.092$, $n = 7$ experiments), perhaps as a result of small sample size. If such a correlation were significant, this would imply that smaller animals are less likely to settle. Presumably, many larvae not recovered in these experiments were either still swimming and/or had metamorphosed elsewhere in the flume. If the former was the case, then higher recovery may have been attained by extending the duration of the experiments. We chose a 24-h maximum experimental

duration because of the potential for post-settlement redistribution, which becomes more likely in longer experiments (e.g., Luckenbach, 1984).

## IMPLICATIONS FOR FIELD DISTRIBUTIONS

This study directly tested the relative importance of bottom topography and substrate type in determining spatial settlement patterns. Results suggest that larvae of Capitella sp. I and Mulinia lateralis are susceptible to relatively subtle near-bottom flow effects such as the circulation in small depressions (of order centimeters). Two extreme views were presented earlier of how selective larvae choose: they may explore substrates independently of flow, or they may be carried along passively, perhaps constrained to near-bottom flow (e.g., Jonsson et al., 1991), and periodically swim or fall out of suspension to test the suitability of the substrate. Results of this study suggest that the latter explanation is more likely appropriate for Capitella sp. I and M. lateralis larvae.

Settlement of Capitella sp. I and Mulinia lateralis is altered by near-bottom flow, suggesting that near-bed flow may be an important mechanism for bringing larvae into contact with a suitable substrate. In the case of Capitella sp. I, however, their competency to settle immediately after release from the brood tube (Dubilier, 1988), their swimming ability and behavior (Butman et al., 1988a) and their ability to delay metamorphosis without significant effects on selectivity (Grassle et al., in press) would tend to make them less vulnerable to hydrodynamic trapping than species that swim poorly and have shorter competency periods. Mulinia lateralis larvae may, however, be

more vulnerable than Capitella sp. I to hydrodynamic trapping. A depression effect was observed for M. lateralis larvae even in small depressions in some instances, suggesting that hydrodynamic trapping may occur even at very small scales indeed. The inability of M. lateralis larvae to delay metamorphosis for longer than a few days (Grassle et al., 1992), combined with a weaker and age-dependent swimming ability (Snelgrove, pers. obs.) may make them even more reliant on near-bed flow to bring them into contact with a suitable sediment. In the field, larval settlement of M. lateralis may occur in very short pulses, on the order of days (Luckenbach, 1984). Thus, if near-bottom currents do not bring larvae into contact with a suitable sediment during their competency period, they may settle in unsuitable areas and experience high post-settlement mortality (Luckenbach, 1984). This may contribute to the highly variable recruitment of M. lateralis observed in the field (Boesch, 1973; Boesch et al., 1976; Virnstein, 1977; Holland et al., 1977).

These results suggest that natural depressions on the sea floor may influence distributions of some species strictly as a result of hydrodynamic trapping and that near-bed hydrodynamics may modify settlement patterns. Because elevated levels of organic matter have been observed in natural depressions (e.g., VanBlaricom, 1982) and around other bottom irregularities such as worm tubes (e.g., Eckman, 1983), it has been difficult to evaluate whether enhanced densities of animals in and around bottom structures result from an active response of settling larvae to the organic matter or from a hydrodynamic effect (e.g., Savidge & Taghon, 1988). Our results suggest that both processes may be involved; relatively strong swimmers such as Capitella sp. I larvae, for example, clearly

are able to respond to elevated organic matter. Depending on age and size distributions, weaker-swimming species like Mulinia lateralis may be more subject to hydrodynamic trapping, irrespective of sediment type.

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# Chapter 3

## Hydrodynamic Enhancement of Invertebrate Larval Settlement in Microdepositional Environments: Colonization Tray Experiments in a Muddy Habitat

## ABSTRACT

To test whether the distribution of settling larvae in muddy habitats is influenced by near-bed hydrodynamics, colonization trays with different trapping characteristics were deployed flush with the ocean bottom at 19-m depth in Buzzards Bay, Massachusetts. The goal of these experiments was to determine whether different densities of settling larvae would be collected under different hydrodynamic conditions. Before deployment, trays were filled with pre-frozen, muddy sediment collected from the site, and some trays (Flush Trays) were filled so that the sediment surface would be flush with that of the ocean bottom when in situ. Other deeper trays (Depression Trays) were filled with a similar volume of sediment so that the sediment surface was approximately 8 cm below that of the surrounding ocean bottom when deployed. This latter treatment created a hydrodynamic regime that would trap passive particles, permitting a test of whether settling larvae at the site would be entrained like passive particles, and thus occur in higher densities in Depression Trays compared with Flush Trays. Experiments were deployed at five different times during the summer of 1990, and were recovered after 3- or 4-d periods depending on the sampling date. Total densities of organisms were higher in Depression Trays compared with Flush Trays on each sampling date, and of the five taxa that were consistently abundant, four were significantly more abundant in Depression Trays (bivalve larvae, gastropod larvae, juvenile Mediomastus ambiseta (Hartman) polychaetes, and nemerteans). Juvenile spionid polychaetes were abundant on only one date, and on that date they were significantly more abundant in Depression Trays. The only abundant taxon that was not significantly more abundant in Depression

Trays was Capitella spp. polychaetes. To determine whether higher numbers in Depression Trays was an active response by settling larvae to elevated organic matter that is often associated with trapping environments such as depressions, some Flush Trays were enriched with Thalassiosira sp. on one of the sampling dates. Densities of organisms in Thalassiosira Trays were either comparable to or lower than those in Flush Trays, suggesting that higher carbon levels do not necessarily promote larval settlement of dominant colonizers at this site over the time scale of these experiments. Furthermore, some of the organisms that were more abundant in Depression Trays were species that normally occur at the site and might therefore be expected to find Flush Trays a suitable environment in which to settle. The most parsimonious explanation for these results is that larvae were passively entrained in Depression Trays, suggesting that near-bed hydrodynamics may, at least in part, determine where larvae settle. These field experiments complement earlier flume studies suggesting that the microdepositional environment of small depressions may result in passive entrainment of settling larvae, indicating that hydrodynamic, as well as behavioral, factors may determine where larvae in muddy habitats initially settle.

## INTRODUCTION

Within the last decade, there has been increasing interest in the role that physical-transport processes may play in determining where larvae of soft-sediment invertebrates settle (e.g., Butman, 1987). Whereas large-scale oceanic circulation has long been known to influence larval distribution (e.g., Thorson, 1961; Scheltema, 1971; Levin, 1983; Banse, 1986), the potential importance of more localized, smaller-scale processes has gained support from the coupling of information on realistic boundary-layer flow and the swimming behavior of planktonic larvae (e.g., Butman, 1986a, 1987). At distances of only a few body lengths above the bottom, larvae of many benthic species may encounter flows that exceed their maximum swimming speeds (Butman, 1986a; Jonsson et al., 1991), suggesting that the potential for hydrodynamic modification of larval settlement is great. Indeed, although controlled flume experiments have demonstrated active habitat selection under realistic flow conditions for several species (e.g. Butman et al., 1988b; Pawlik et al., 1991; Grassle et al., 1992a,b; Butman & Grassle, 1992), there is also evidence from these flume studies that both active and hydrodynamic processes may influence settlement (e.g., Pawlik et al., 1991; Butman & Grassle 1992; Snelgrove et al., 1993; Pawlik & Butman, submitted).

Because many planktonic larvae may be poor swimmers, it is perplexing that many soft-sediment species from a variety of habitats are associated with a given sediment type (e.g., see reviews of Gray, 1974; Rhoads, 1974). Although the mechanism responsible for this association is poorly understood (Snelgrove & Butman,

submitted) several explanations have been proposed, including variation in carbon supply (e.g. Sanders, 1958), amensalistic interactions (Rhoads & Young, 1970), and larval predation (e.g., Woodin, 1976). Consistent experimental evidence to support these explanations is lacking, however, and an alternative explanation is that near-bed hydrodynamics may sort some planktonic larvae in a manner similar to sediment sorting (e.g., Butman, 1987). This mechanism could result in sediment-specific distributions where hydrodynamics, rather than the bottom sediments per se, limit the distribution of species.

In soft-sediment habitats, the role of hydrodynamics is particularly difficult to evaluate because different sedimentary environments are generally associated with different flow regimes, which in turn may result in differences in nutrient, detritus, and larval supply (e.g., Jumars & Nowell, 1984). Thus, separating out the relative effects of all of these variables on a large scale is a near impossible task. On a small scale, field experiments have been conducted that utilize structures such as animal tubes or seagrass shoots to create regions of enhanced deposition and erosion over scales of millimeters to centimeters. Experimental manipulations of such structures have been used to demonstrate that small-scale hydrodynamics have an important effect on recruitment in intertidal sandflats (Eckman, 1979, 1983). An alternative approach for testing hydrodynamic effects on settling larvae is to use collection devices such as sediment traps (Butman, 1989) or bottom depressions (e.g., Savidge & Taghon, 1988) to determine whether collection of colonizers approximates that of passive particles. Cavities such as depressions and empty cylinders create a flow regime that tends to trap

passive particles because of a small recirculating eddy that forms within the container, increasing particle retention time and decreasing the probability of particle resuspension (trapping containers are discussed at length in Butman et al., 1986 and Snelgrove et al., 1993).

Several studies have demonstrated enhanced densities of organisms in natural depressions compared with ambient sediments (e.g., VanBlaricom, 1982; Oliver & Slattery, 1985), but enhanced accumulation of organic matter was also noted. Thus, it was not possible to determine whether settlement was passive, as a result of passive entrainment in depressions, or whether organisms were actively responding to elevated organic matter. Furthermore, the results of these studies may not be applicable in all habitats because the majority of these studies were conducted in high-energy environments, where trapping characteristics may be more complicated and sediment movement may modify the shape and trapping characteristics of depressions more quickly than in lower-energy habitats (e.g. VanBlaricom, 1982; Savidge & Taghon, 1988; Emerson & Grant, 1991). Studies in high-energy environments have also tended to focus on recruitment rather than initial settlement, in part because many species lacked a planktonic larval stage at the particular study sites (e.g., Eckman, 1979, 1983; Savidge & Taghon, 1988). Indeed, the high energy of sandflat habitats may dramatically influence colonization through bedload transport of post-larval and adult individuals (e.g., Savidge & Taghon, 1988; Emerson & Grant, 1991; Hall et al., 1991). Redistribution of settled individuals may be less likely in lower-energy environments because their critical erosion velocities (shear velocity required to initiate particle

motion, see Miller et al., 1977) are less likely to be exceeded.

The goal of the present study is to test whether enhanced settlement is observed in small depressions compared with flush treatments where a muddy substrate is available to settling larvae. To minimize the effect of accumulation of organic matter in depressions compared with flush treatments, the study was undertaken in a relatively low-energy, muddy environment (20-m depth) over a relatively short time scale (3 days). This short time scale also minimized the likelihood of post-settlement interactions between colonizing species, and was geared towards evaluating settlement rather than recruitment. These field experiments were designed to complement flume studies that demonstrated higher settlement of Capitella sp. I and Mulinia lateralis in small depressions than in flush treatments, when the confounding effects of suspended sediment and organic matter were absent (Snelgrove et al., 1993).

## METHODS

Field experiments were conducted at "Station R", a well-studied (e.g., Sanders, 1958; Moore, 1963; Rhoads & Young, 1970; Farrington et al., 1977) muddy habitat in Buzzards Bay, Massachusetts, U.S.A. (41°29.25'N, 70°53.8'W, 20-m depth, Fig. 1). Experiments were deployed at approximately 2-week intervals throughout the summer of 1990 for periods of 3 or 4 days (Table I). All experiments were conducted using mud collected at Station R in April, 1990 with a van Veen grab. The upper 2-3 cm of

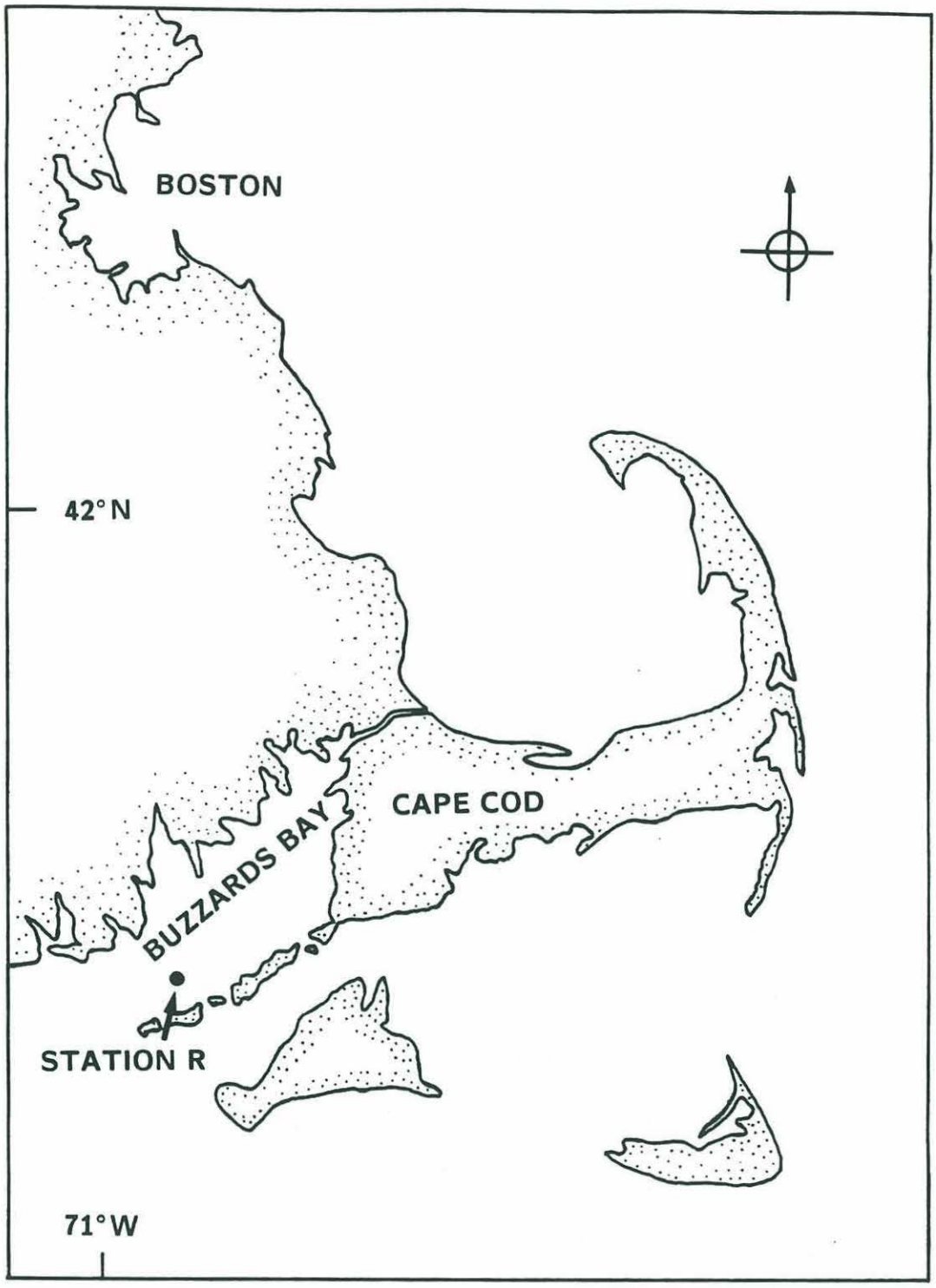


Figure 1. Chart showing location of Station R in relation to Cape Cod and Buzzards Bay.

TABLE I
Schedule of field deployments and treatments

| Date Recovered | Duration | Treatments |
|---|---|---|
| July 20 | 3 days | 4 Flush Trays |
| | | 4 Depression Trays |
| August 10 | 3 days | 3 Flush Trays |
| | | 3 Depression Trays |
| August 20 | 3 days | 4 Flush Trays |
| | | 4 Depression Trays |
| August 31 | 3 days | 4 Flush Trays |
| | | 4 Depression Trays |
| September 11 | 4 days | 2 Flush Trays |
| | | 4 Depression Trays |
| | | 3 Thalassiosira Trays |

sediment from multiple grabs was homogenized, frozen and then thawed the day before it was needed for field experiments.

Sediment trays were constructed from a large, circular Delrin plate (40-cm diameter, 2-cm thick) with a central opening 11.3 cm in diameter. This plate was modified in one of two ways (Fig. 2). A removable cup with 20-µm mesh sides and bottom could be aligned with the central opening and attached to the underside of the plate, resulting in a 10-cm deep central cup (hereafter this design is referred to as Depression Trays). This design has been described in greater detail elsewhere (Snelgrove et al., 1992). Alternatively, 20-µm mesh was attached directly to the underside of the plate with a retaining ring, resulting in a 2-cm deep cup (hereafter this design is referred to as Flush Trays). The 20-µm mesh in Depression and Flush Trays allowed porewater exchange. Sediment was added to the Flush Trays so that the sediment surface was flush with the Delrin plate. A similar volume of sediment was added to the Depression Trays, resulting in a depression 11.3 cm in diameter and approximately 8 cm deep. For both designs, sediment was added to the central well, resulting in a sediment surface area of 100 $cm^2$.

While conducting preliminary experiments, it became apparent that large clumps of algae were often entrained in Depression Trays, even over a time period of several days. To eliminate this problem, mesh (0.5-cm square opening) was placed above the sediment surface flush with the Delrin plate so that it would not interfere with bottom flow. This prevented large clumps of algae from entering Depression Trays and may also have reduced the impact of predation. Identical mesh was also placed on Flush

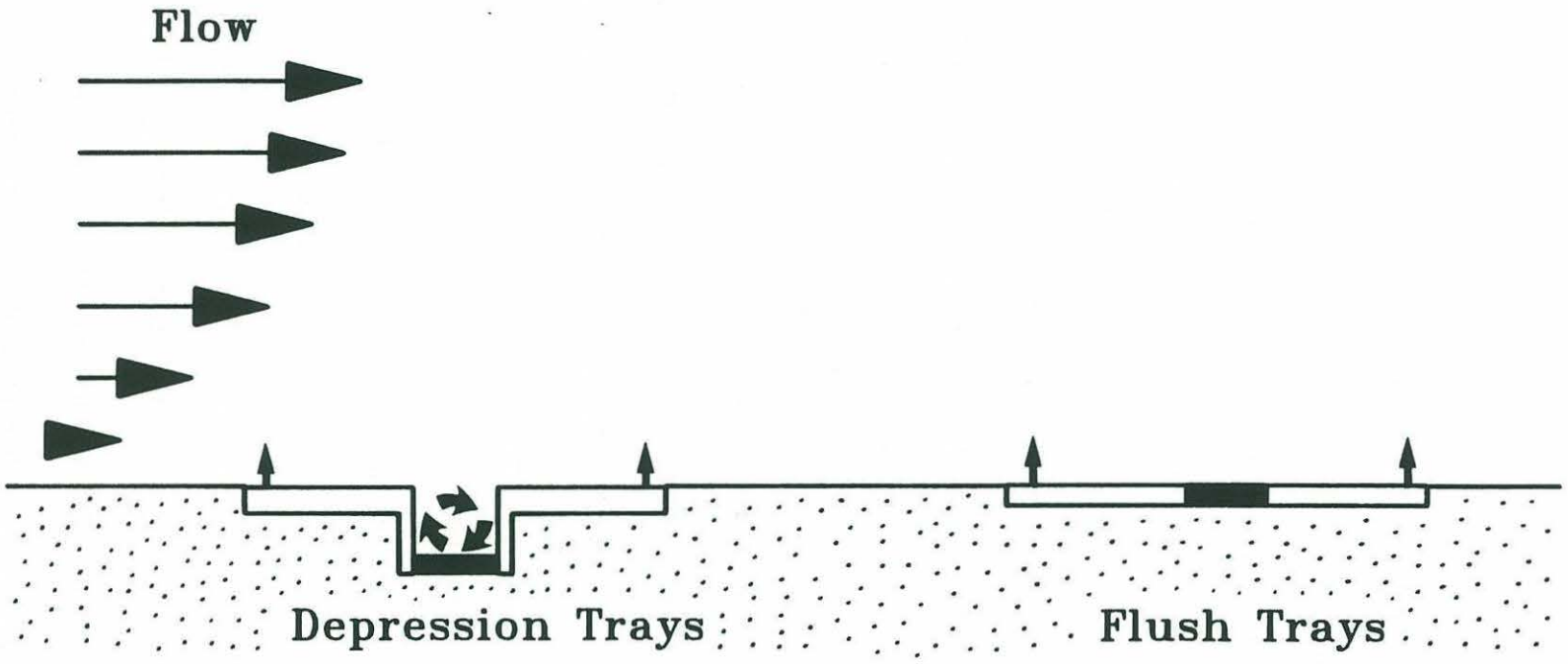


Figure 2. Schematic representation of tray deployments. Black area shows prefrozen sediment in trays and stippled areas indicate ambient sediment. The small arrows protruding above the trays are exaggerated in size and represent posts that lock the recovery lid in place during transport to the surface. Depression and Flush Trays are 10 cm and 2 cm deep, respectively, and the diameter of the sediment cup is 11.3 cm.

Trays.

A sealing lid was used to contain the sediment while trays were transported to the bottom on a rack that contained eight trays. SCUBA divers removed trays from the rack and placed them flush with the sea floor so that there would be a smooth flow transition between the ambient sediment, the Delrin plate and, in the case of Flush Trays, the contained sediment (Fig. 2). Although Depression Trays were also flush with the ambient sediment surface, the sediment in the tray was approximately 8 cm below that of the ambient sediment, resulting in a trapping environment. For each experiment, divers deployed the tray treatments in a haphazard sequence along a transect that ran approximately northwest-southeast, perpendicular to the dominant tidal flow. Trays were placed at least 1 m apart, and once in place, the sealing lids were removed only after the sediment resuspended by diver activity had largely cleared.

For one of the experiments (September 11), an additional treatment was added to determine whether enhanced numbers in depressions was an active response to elevated organic carbon. Thalassiosira sp. paste was mixed through the top 1.5 cm of 3 Flush Trays (hereafter referred to as Thalassiosira Trays) to produce an approximate enrichment of 1% by dry weight organic carbon. Other than the algal addition, Thalassiosira Trays were treated as described for Flush Trays.

After 3-4 days, divers returned to the trays and used a meat baster to carefully blow away any sediment that had settled on the Delrin plate. Sealing lids were then attached to each of the trays before transport to the surface, ensuring that sediment and colonizers would not be lost. Not all trays were recovered intact and these were

discarded, resulting in less than four replicates in some instances (Table I). Samples were processed over nested 300- and 63-µm sieves, preserved in 10% buffered formalin, and later transferred to 80% ethanol with Rose Bengal stain. The nested sieves were used to separate colonizing adults from larvae; for the polychaetes, however, this proved to be ineffective (many recently-settled juveniles were retained on the 300-µm screen) and unnecessary (adults were rare). For bivalves, some individuals were too large to have recently settled. Therefore, the 63-µm fraction, which contained only recently-settled individuals, was analyzed separately and compared with the result obtained from the combined fraction (see below).

During the initial sorting of the samples, it became clear that most of the colonizers were recently-settled juveniles that could not be identified to species. Almost every bivalve that could be identified (often near 50% of total bivalves collected) was Nucula annulata. Many of the bivalves that could not be identified may also have been this species, therefore it was not possible to accurately estimate the number of N. annulata present. Thus, the bivalve totals used in the analyses consist primarily of this species, but also include other species. Virtually none of the gastropods, nemerteans and spionids were sufficiently large to identify to species, or in some cases to family, and the totals certainly contain several species. Testing the passive deposition hypothesis for a broad taxon (e.g., combined bivalves) is a reasonable approach because the swimming behavior of different species within a broad taxon is expected to be roughly comparable among species (e.g., Jonsson et al., 1991; Grassle et al., 1992b), and individuals within the groupings were morphologically very similar.

## HYPOTHESES FOR TRAY EXPERIMENTS

All sediment tray experiments were designed to test the hypothesis that available larvae are deposited on the bottom as passive particles and should, therefore, occur in higher numbers in Depression Trays compared with Flush Trays. Because this experimental design does not eliminate the possibility that higher numbers in Depression Trays could result from an active response by settling larvae to elevated carbon levels, an additional experiment with Thalassiosira enrichment was performed to determine whether elevated densities of colonizers would be observed in Thalassiosira Trays (with greatly elevated carbon content) and Depression Trays compared with Flush Trays. Because very different larval taxa (e.g., bivalves and polychaetes) may not necessarily be influenced by hydrodynamic manipulation in a similar way, analysis of total individuals was not considered meaningful and the hypothesis of comparable settlement in Flush Trays and Depression Trays (and Thalassiosira Trays for the latter analysis) was tested separately for those taxa of organisms (i.e., bivalves, gastropod larvae, Mediomastus ambiseta juveniles, Capitella spp. juveniles, spionid juveniles, and nemerteans) that were collected in sufficient numerical abundance to be compared meaningfully.

## STATISTICAL ANALYSIS

Larval settlement patterns for the dominant taxa Mediomastus ambiseta, Capitella spp., spionids, nemerteans, bivalves and gastropods were analyzed using the ANOVA model $y = \mu + \text{Treatment} + \text{Date} + \text{Treatment} \times \text{Date} + \text{Error}$, where $\mu$ is the constant,

Treatment is the main effect (i.e., testing for differences between Flush Trays and Depression Trays), and Date is a blocking factor to account for temporal variation in larval availability during the summer. Although one deployment (Sept. 11) extended over 4 days rather than 3 (Table 1), densities in this experiment were lower than in some 3-day deployments. This suggests that larval supply was more important than the duration of the experiment, and all dates were therefore compared in a single analysis. For this model, the Date effect was random and the Treatment effect was fixed. Data were log (x+1) transformed to homogenize variances between treatments. All five experimental dates were included in this analysis; however, Thalassiosira Trays were not included because they were only represented in a single experiment. Thus, the September 11, 1990 experiment was also analyzed separately (with the Thalassiosira Trays) using the ANOVA model $y = \mu + \text{Treatment} + \text{Error}$. Treatment is a fixed main effect with three levels (Flush Trays, Thalassiosira Trays, and Depression Trays). Because a significant Treatment effect was observed in this analysis, means were compared with a Tukey's HSD Multiple Comparisons test.

## RESULTS

Trays were colonized by a variety of taxa including bivalves, gastropods, polychaetes, nemerteans, enteropneusts, amphipods and decapods. On all 5 of the sampling dates, total densities of organisms in Depression Trays were higher than those in Flush Trays (Fig. 3). Variation between dates was quite substantial, and the relative contribution of different taxa changed considerably through the summer. Because

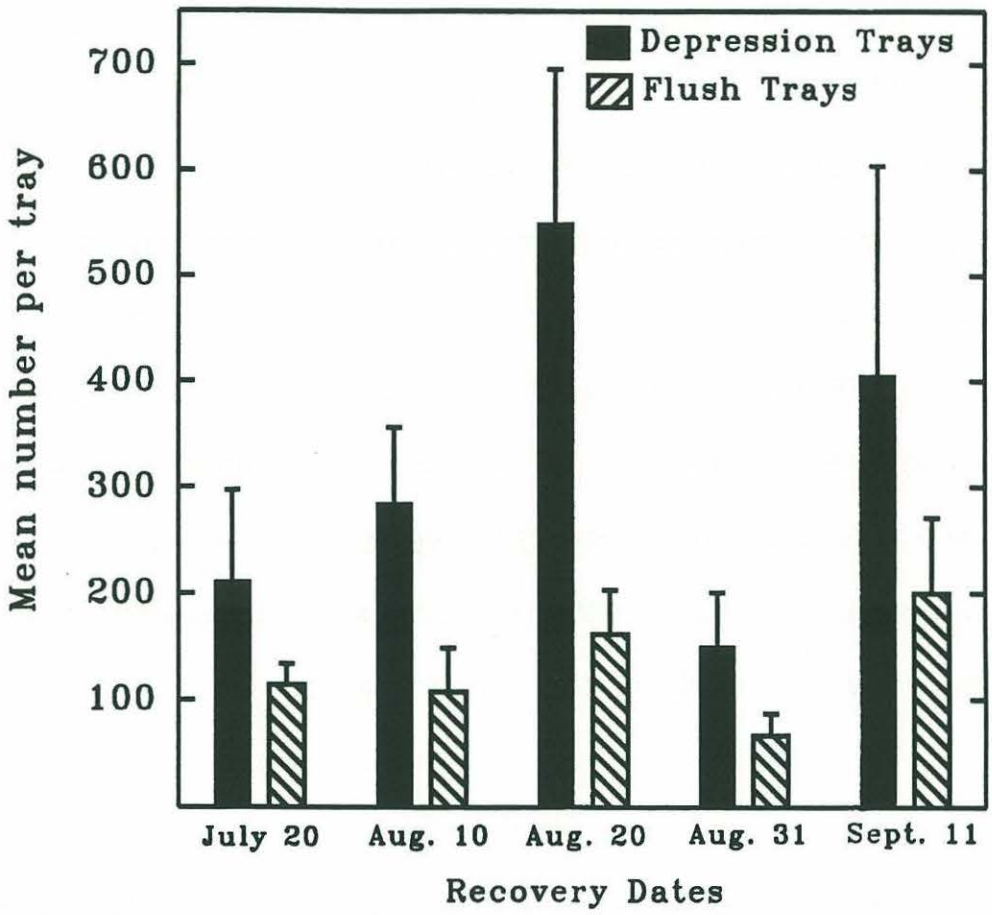


Figure 3. Results for total densities of organisms (i.e., all taxa combined) collected in colonization trays over the 5 experimental dates. Vertical bars denote mean values and lines above them denote 1 standard deviation. Number of replicates on which estimate is based ranged from 2-4, and are given in Table I.

larvae of different taxa have very different swimming behavior and because the relative abundances of each taxa varied through the summer, data on each of the abundant taxa were analyzed separately. Many taxa were absent or represented by only a few individuals on most sampling dates, however, six taxa (bivalves, gastropod larvae, Mediomastus ambiseta juveniles, Capitella spp. juveniles, spionid juveniles and nemerteans) were sufficiently abundant to warrant statistical comparison.

For five of the six abundant taxa (Table II) there was large variability in the numbers of individuals of each species collected over time (Figs. 4,5). Nonetheless, the Treatment x Date effect was not significant for any of the dominant taxa except spionid juveniles. Because of the significant Treatment x Date effect for spionid juveniles, treatments were compared for each date separately.

Analysis of bivalves, gastropod larvae, Mediomastus ambiseta juveniles, spionid juveniles and nemerteans indicated a significant Treatment effect for each taxon (Table II), with significantly more individuals collected in Depression Trays than in Flush Trays (Figs. 4,5). In the analysis of bivalves, individuals that were clearly post-larvae were included in the analysis because there was no objective way to distinguish between recently settled versus older individuals. A separate analysis that excluded bivalves that were retained on a 300-μm screen revealed an identical result, with significantly higher densities of bivalves in Depression Trays than in Flush Trays. This result suggests that higher numbers in Depression Trays was a result of higher densities of larvae rather than post-larvae, because most of the individuals included in this analysis were within the size range for settling larvae. The only abundant taxon with no significant Treatment

TABLE II

ANOVA results for dominant taxa settling in Flush and Depression Trays on all experimental dates. Densities were log (x+1) transformed to homogenize variances. Thalassiosira trays were not included because they were deployed on only one Date.

| Source | df | SS | F | p |
|---|---|---|---|---|
| **Bivalve spp.** | | | | |
| Date | 4 | 6.471 | 8.065 | 0.000*** |
| Treatment | 1 | 11.200 | 39.133 | 0.003** |
| Date x Treatment | 4 | 1.145 | 1.427 | 0.253 |
| Error | 26 | 5.215 | | |
| **Gastropod spp.** | | | | |
| Date | 4 | 24.503 | 16.552 | 0.000*** |
| Treatment | 1 | 11.456 | 22.771 | 0.009** |
| Date x Treatment | 4 | 2.028 | 1.370 | 0.272 |
| Error | 26 | 9.623 | | |
| **Mediomastus ambiseta** | | | | |
| Date | 4 | 13.363 | 15.406 | 0.000*** |
| Treatment | 1 | 3.606 | 11.407 | 0.028* |
| Date x Treatment | 4 | 1.265 | 1.458 | 0.244 |
| Error | 26 | 5.638 | | |
| **Capitella spp.** | | | | |
| Date | 4 | 33.002 | 21.434 | 0.000*** |
| Treatment | 1 | 1.900 | 3.708 | 0.126 |
| Date x Treatment | 4 | 2.050 | 1.331 | 0.285 |
| Error | 26 | | | |
| **Spionidae spp.** | | | | |
| Date | 4 | 12.245 | 9.535 | 0.000*** |
| Treatment | 1 | 6.858 | 6.100 | 0.069 |
| Date x Treatment | 4 | 4.497 | 3.502 | 0.020* |
| Error | 26 | 8.348 | | |

TABLE II (cont.)

ANOVA results for dominant taxa settling in Flush and Depression Trays on all experimental dates. Densities were log (x+1) transformed to homogenize variances. Thalassiosira trays were not included because they were deployed on only one Date.

| Source | df | SS | F | p |
|---|---|---|---|---|
| **Nemertean spp.** | | | | |
| Date | 4 | 3.871 | 2.252 | 0.091 |
| Treatment | 1 | 9.950 | 35.506 | 0.004** |
| Date x Treatment | 4 | 1.121 | 0.652 | 0.631 |
| Error | 26 | 11.175 | | |

***p≤0.001, **p≤0.01, *p≤0.05

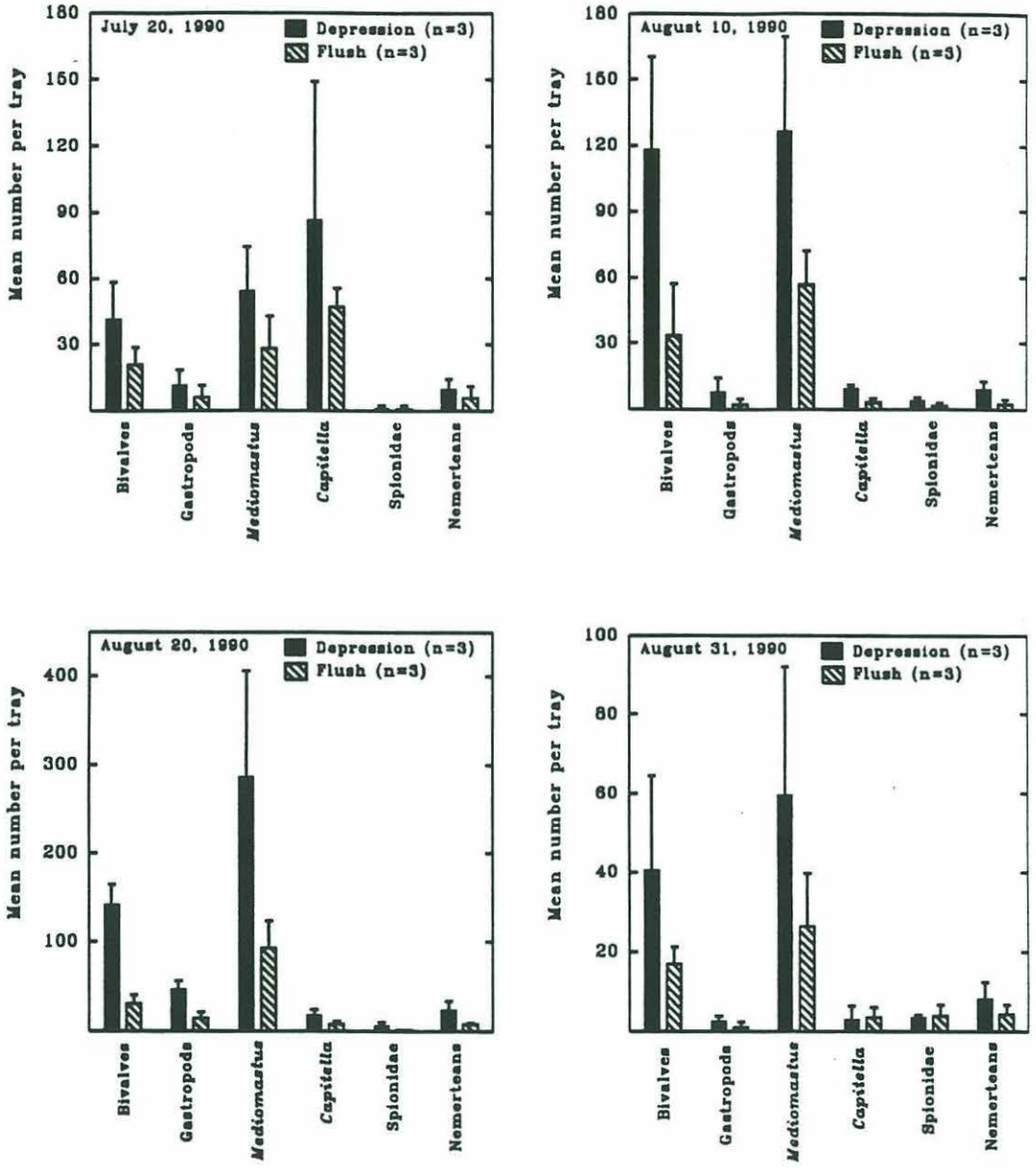


Figure 4. Results for the 6 taxa that were relatively abundant on all 5 experimental dates. Vertical bars denote mean values and lines above them denote 1 standard deviation.

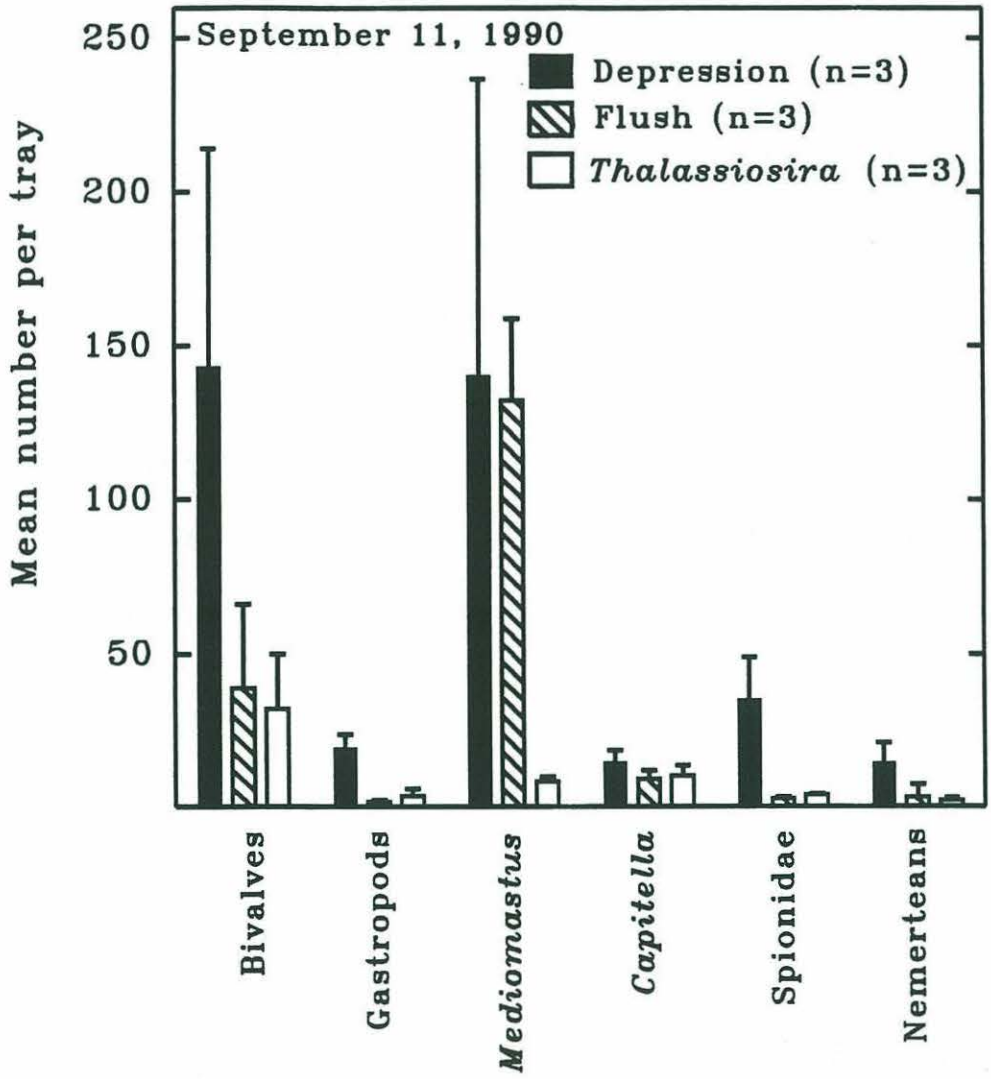


Figure 5. Results from the September 11 experiment where Thalassiosira-enriched trays were deployed with Depressions and Flush Trays. Shown are the 6 most abundant taxa, with vertical bars denoting mean values and lines above them denoting 1 standard deviation.

effect was Capitella spp. Densities of Capitella spp. were higher in Depression Trays than Flush Trays on four of the five sampling dates, but on most of the sampling dates, numbers were low.

In the comparison of the Flush and Depression Tray results with the Thalassiosira Trays (Fig. 5), significantly more bivalves, gastropod larvae, Mediomastus ambiseta juveniles, spionid juveniles and nemerteans were collected in Depression Trays compared with Thalassiosira Trays (Table III). Densities in Thalassiosira Trays and Flush Trays did not differ significantly for any taxa except M. ambiseta, which was less abundant in Thalassiosira Trays. Thus, there is no evidence that the elevated carbon levels in Thalassiosira Trays attracted colonizers. Mean densities in Depression Trays were higher than in Flush Trays for all six of the abundant taxa, but the difference was significant only for gastropod larvae and spionid juveniles. The lack of significant differences between Flush Trays compared with Depression Trays may be a result of the low statistical power of the comparison because Flush Trays were represented by only two replicates.

## DISCUSSION

Consistently higher densities of organisms in Depression Trays compared with Flush Trays for most dominant taxa strongly suggests that fine-scale bottom flow may significantly influence where larvae at Station R initially settle. The effects of near-bed hydrodynamics on recruitment of macrobenthos has been studied most intensively in relatively high-energy, sandflat communities (e.g. Eckman, 1979, 1983; Savidge &

TABLE III

ANOVA results for dominant taxa settling in Flush, Depression and Thalassiosira Trays in experiment ending on September 11, and results of Tukey-Kramer tests for significant treatment effects Densities were log (x+1) transformed to homogenize variances.

| Source | df | SS | F | p |
|---|---|---|---|---|
| **Bivalve spp.** | | | | |
| Treatment | 2 | 4.530 | 6.741 | 0.029* |
| Error | 6 | 2.016 | | |
| **Gastropod spp.** | | | | |
| Treatment | 2 | 7.548 | 22.291 | 0.002** |
| Error | 6 | 1.016 | | |
| **Mediomastus ambiseta** | | | | |
| Treatment | 2 | 13.636 | 22.146 | 0.002** |
| Error | 6 | 1.847 | | |
| **Capitella spp.** | | | | |
| Treatment | 2 | 0.334 | 1.693 | 0.261 |
| Error | 6 | 0.591 | | |
| **Spionidae spp.** | | | | |
| Treatment | 2 | 9.864 | 50.461 | 0.000*** |
| Error | 6 | 0.586 | | |
| **Nemertean spp.** | | | | |
| Treatment | 2 | 2.954 | 6.590 | 0.031* |
| Error | 6 | 0.448 | | |

*$p \leq 0.05$, **$p \leq 0.01$, ***$p \leq 0.001$

TABLE III (cont.)
ANOVA results for dominant taxa settling in Flush, Depression and Thalassiosira Trays in experiment ending on September 11, and results of Tukey-Kramer tests for significant treatment effects. Densities were log (x+1) transformed to homogenize variances.

| Tukey-Kramer test | **Bivalve spp.** | | |
|---|---|---|---|
| Treatment | Depression | Flush | Thalassiosira |
| Mean | 143.0 | 36.0 | 31.7 |

| | **Gastropod spp.** | | |
|---|---|---|---|
| Treatment | Depression | Thalassiosira | Flush |
| Mean | 19.75 | 3.3 | 1.0 |

| | **Mediomastus ambiseta** | | |
|---|---|---|---|
| Treatment | Depression | Flush | Thalassiosira |
| Mean | 139.8 | 131.5 | 8.0 |

| | **Spionidae spp.** | | |
|---|---|---|---|
| Treatment | Depression | Thalassiosira | Flush |
| Mean | 34.8 | 3.7 | 2.5 |

| | **Nemertean spp.** | | |
|---|---|---|---|
| Treatment | Depression | Flush | Thalassiosira |
| Mean | 14.2 | 3.0 | 2.0 |

Taghon, 1988; Emerson & Grant, 1991), and these studies have demonstrated that near-bed hydrodynamics do indeed influence the distributions of macrobenthic organisms. Of these experiments, the most comparable to the present study are those of Savidge & Taghon (1988) and Emerson & Grant (1991), who used trapping environments to test for enhanced larval and post-larval colonization under conditions likely to trap passive particles. Higher densities of most taxa were observed in artificial pits compared with defaunated flush treatments, and for many taxa the numbers in depressions exceeded those in undisturbed ambient sediment (Savidge & Taghon, 1988). Because densities of organisms did not correlate well with factors such as chlorophyll or carbon content of sediments, they concluded that passive advection of colonizers into depressions was a more likely explanation for higher densities in depressions. Many of the individuals that occurred in depressions were not recently settled individuals, and passive, post-larval redistribution of bivalves was shown to commonly occur in another sandflat community (Emerson & Grant, 1991). Similarly, studies of natural depressions (e.g., VanBlaricom, 1982; Oliver & Slattery, 1985) and ripple troughs (Sameoto, 1969; Fenwick, 1984), have shown that some taxa occur in higher densities in trapping environments compared with ambient sediment. Other studies, however, have found lower densities of organisms associated with natural depressions (e.g. Reidenauer & Thistle, 1981; Oliver et al., 1985; Hall et al., 1991), even several weeks after defaunation has taken place. Most of the organisms studied in all of these experiments were adults or juveniles.

Although differences in the ambient faunal community and mode of defaunation

likely contributed to the inconsistencies in these studies of natural disturbances, variability may, in part, reflect the complex nature of flow over depressions. As flow moves over a depression, the boundary layer detaches at the upstream edge of the depression, and a small recirculating eddy forms within the depression. Pulses of fluid enter at the downstream edge of the depression and leave at the upstream edge (e.g. Rockwell & Naudascher, 1978), resulting in the entrainment of passive particles within the depression. In deep depressions (aspect ratio or depression height/depression diameter >> 1), a series of vertically stacked eddies form (e.g., Weiss & Florsheim, 1965), and in shallow depressions (aspect ratio << 1), a growing boundary layer may form on the floor of the depression and create a more complex flow. Although the flow over depressions with an aspect ratio near 1 may appear very similar over a range of flow Reynolds numbers (e.g. Haugen & Dhanak, 1966; Pan & Acrivos, 1967), entrainment and deposition of passive particles are two separate processes. Boundary shear stress within a depression may actually exceed that in the ambient environment (Roshko, 1955), and this may be particularly important in high-energy environments where critical erosion velocities of passive particles (i.e., shear velocity required to initiate particle motion; e.g., Miller et al., 1977) are more likely to be exceeded. Thus, although passive particles may be entrained in depressions, they may not accumulate under some hydrodynamic conditions. This explains, in part, why light particles accumulate in depressions under some flow conditions (Risk & Craig, 1976) but heavy particles accumulate in others (e.g. Nelson et al., 1987). Indeed, Emerson & Grant (1991) noted that detritus accumulated in their "depressions" only during part of the tidal

cycle. Thus, an absence of elevated densities of organisms in "trapping" environments in some intertidal sandflat studies may reflect the complex relationship between entrainment and deposition in depressions. Similarly, shallow depressions have been observed to have lower densities of organisms than deep depressions (Nerini & Oliver, 1983), perhaps again reflecting differences in particle trapping characteristics. Thus, the complex nature of flow over the depressions in these sandflat studies may have resulted in differences in deposition of passive larvae or differences in deposition of organic matter to which larvae actively responded.

Because of the complex hydrodynamics associated with high-energy environments, results from intertidal sandflats may not accurately reflect hydrodynamic effects on larval settlement in muddy habitats. There are several lines of evidence that suggest the Depression Trays should not only entrain more passive particles than Flush Trays but also retain them. Extrapolation from existing sediment trap studies (e.g., Lau, 1979; Butman, 1986b) suggests that particles in the size range of settling larvae will not be resuspended in Depression Trays over most flow conditions that occur in Buzzards Bay, and flume studies with larval mimics conducted under flow conditions typical of Buzzards Bay found that numbers of larval mimics tended to be slightly higher than in flush treatments (Snelgrove et al., 1993). Furthermore, in these flume experiments no sediment resuspension was noted, and resuspension of larvae was therefore unlikely because near bottom flow should influence passive larvae and light silt particles in a similar way (see Butman, 1987). Perhaps the most compelling evidence for retention of passive particles in Depression Trays was a failed experiment conducted in October,

1991. After deploying an experiment comparable to those described here, high winds delayed recovery of the experiment until 6 d after trays were deployed. This experiment was not analyzed because the Depression Trays were more than half-full of fine sediments. Presumably, sediment resuspended by the storm conditions had been entrained and deposited in Depression Trays, suggesting that Depression Trays did indeed act as traps for passive particles.

The elevated densities of total organisms and significantly higher numbers of five of the six most abundant taxa in Depression Trays compared with Flush Trays suggest that settling larvae (and some post-larvae) were passively entrained in Depression Trays by near-bed hydrodynamics. This does not suggest, however, that individuals could not have escaped from Depression Trays had the substrate been unsuitable. Thus, near-bed hydrodynamics appear to have influenced colonization; however, the role of active processes cannot be evaluated in this study because the substrates in Flush and Depression Trays were equally favorable. In a related flume study, more larvae of the polychaete Capitella sp. I settled in small depressions than in comparable flush sediments, although they were often able to "escape" from depressions if the substrate was unsuitable (Snelgrove et al., 1993). In a similar flume experiment, the ability of M. lateralis larvae to "escape" from depressions containing an unsuitable substrate was somewhat variable and may have been reduced in older, heavier larvae. These flume results suggest that both behavioral and hydrodynamic components were involved in larval settlement for these species. In the present field study, the sediment in Depression Trays and Flush Trays was very similar, and larval encounter with the

Depression Tray sediment was likely enhanced by passive entrainment. Thus, hydrodynamic effects influence the likelihood that a larva will encounter a suitable substrate, but behavioral components may also help determine whether larvae settle. Flume experiments designed to study substrate selection by settling larvae suggest that active selection by larvae is often (Butman et al., 1988b; Butman & Grassle, 1992; Grassle et al., 1992a,b; Snelgrove et al., 1993), but not always (Bachelet et al., 1992) an important component as well.

Results from various taxa in these experiments provide an interesting contrast with previous studies that have utilized passive trapping characteristics to evaluate the role of near-bed hydrodynamics. The passive redistribution of settled Mya arenaria spat by bedload transport was shown to be an important controlling mechanism in intertidal (Emerson & Grant, 1991), and the presence of some fairly large individuals of Nucula annulata in the present study (pers. obs.) suggests that some redistribution by bedload transport may also occur at Station R. Alternatively, these large individuals may have moved into trays, however, the majority of bivalves collected were very small. Thus, the majority of the colonizing bivalves were larvae carried in suspension. The results of this field study are also consistent with a flume study using flow conditions similar to those in Buzzards Bay that showed significant enhancement of larval settlement in depressions by another bivalve Mulinia lateralis (Snelgrove et al., 1993).

Bivalves, juvenile spionids, Mediomastus ambiseta, and larval gastropods were more abundant in sediment traps with higher collection efficiency compared to containers with lower efficiency in Butman's (1989) study. These findings are similar

to those shown here, and the general consistency between her results and those observed in the present study may reflect the similar flow conditions and muddy habitat in which experiments were performed.

Based on flume studies on settlement of Capitella sp. I in depressions versus flush treatments (Snelgrove et al., 1993), higher densities of Capitella spp. might be expected in Depression Trays compared with Flush Trays. Although numbers of Capitella spp. were generally higher in Depression Trays than Flush Trays, the result was not significant, perhaps because of the generally low settlement.

An alternative explanation for the higher numbers of dominant taxa observed in Depression Trays compared with Flush Trays in the present study is that settling larvae actively responded to elevated organic matter that is often associated with depressions (e.g., VanBlaricom, 1982; Oliver et al., 1985; Savidge & Taghon, 1988). Although there is little doubt that Depression Trays accumulated organic matter during the course of these experiments, passive deposition is a more parsimonious explanation for enhanced densities in Depression Trays for several reasons. First, trays that were enriched with Thalassiosira sp. in early September were colonized by relatively few individuals. If organic enrichment resulted in elevated densities in Depression Trays, then rapid colonization of Thalassiosira Trays would also be expected over the same time scale. It is possible, however, that the Thalassiosira sp. was not attractive to the species that were abundant in Depression Trays, but they may have responded to other forms of organic matter that accumulated in Depression Trays. This scenario is doubtful, however, given the types of organisms that were most abundant. The bivalve colonizers

were predominantly Nucula annulata, a species that is not known to be opportunistic and occurs in high densities at Station R (e.g., Sanders, 1958; pers. obs.). Thus, there is no reason to expect that Flush Trays would not have been a suitable sediment for settling larvae, and Depression and Flush Trays should have been equally attractive. Mediomastus ambiseta can also occur at Station R in high densities (R.B. Whitlatch, pers. comm), and is, therefore, likely to have found Flush Trays and Depression Trays equally suitable. The most compelling evidence for hydrodynamic modification comes from flume studies on related taxa (Snelgrove et al., 1993), where elevated densities of organisms were observed in depressions compared with flush treatments. Filtered seawater was used in these experiments to minimize any possible accumulation of organic matter in depressions. Thus, in the absence of any suspended sediment or organic material, the bivalve Mulinia lateralis and the polychaete Capitella sp. I were found to be more abundant in depressions compared with flush treatments of an identical sediment treatment under flow conditions roughly comparable to those in this field study (Snelgrove et al., 1993). Given that these flume results may be best explained by hydrodynamic entrainment, the most parsimonious explanation for the enhanced densities observed in Depression Trays at Station R is that larvae were passively entrained in depressions.

The significant Date effect for five of the six abundant taxa is not surprising, given that larval supply was not expected to be consistent over the time period of the experiments. There is, however, evidence suggesting that flow conditions were an important aspect of this variability. Many of the abundant taxa also showed a highly

significant positive correlation with each other (unpublished data). Although it is possible that unrelated taxa of larvae were synchronously available over time scales of weeks, a more likely explanation is that flow conditions were variable between different dates, and that settlement (and passive entrainment) was greater when bottom currents carried more competent larvae from a variety of taxa across the experimental trays.

Although coarse mesh was placed flush with the trays to prevent the accumulation of large clumps of algae, it may have had other effects as well. Large predators, which have an important impact on organisms in natural depressions in sandflat communities (e.g. VanBlaricom, 1982; Nerini & Oliver, 1983; Oliver et al., 1985; Savidge & Taghon, 1988), were likely excluded from trays in the present study. Trays may also have excluded organisms that migrate through the sediment (e.g., Smith & Brumsickle, 1989). Thus, as a mimic for natural depressions trays are a poor analog, but they were not deployed to study the dynamics of natural depressions. The goal of these experiments was not to study the effects of natural disturbance on benthic communities but to manipulate near-bottom flow to determine whether fine-scale processes modify larval settlement. The mesh may also have increased passive entrainment of particles into Depression Trays by enhancing sedimentation (e.g., see Butman, 1986b, 1989), an effect that would not have occurred with Flush Trays where the mesh was flush with the sediment surface. Given the goal of the Depression Tray manipulation, however, enhanced trapping characteristics for Depression Trays are, in fact, desirable.

Virtually all of the organisms that were collected in Flush and Depression Trays

were recently settled bivalves and polychaetes. This is in stark contrast to sandflat macrofaunal studies, where depressions may be colonized by high densities of crustaceans (e.g. VanBlaricom, 1982; Oliver & Slattery, 1985) and where redistribution of post-larval bivalves is important (Emerson & Grant, 1991). Although some polychaetes and bivalves may have been missed because a relatively coarse sieve was used to process samples (e.g., VanBlaricom, 1982; Oliver & Slattery, 1985), the abundance of larger motile fauna may reflect a fundamental difference between high-energy sandflat environments and more quiescent muddy habitats. Sandflat communities tend to be characterized by strongly-swimming crustaceans (e.g. Oliver et al., 1985) and bedload redistribution of settled individuals (e.g. Emerson & Grant, 1991), whereas in muddy communities, colonization of new habitat may be accomplished largely by planktonic larvae. Though it may be argued that trays such as those used in the present study prevent horizontal immigration of adults through the sediment (e.g., Smith & Brumsickle, 1989), a roughly similar tray design was used by Emerson & Grant (1991), who emphasized the importance of post-settlement redistribution.

Natural depressions of many shapes and sizes may be formed through a variety of biological activities such as feeding by whales and walruses (e.g., Oliver & Slattery, 1985; Oliver et al., 1985), fish (e.g., Reidenauer & Thistle, 1981, VanBlaricom, 1982) or crabs (e.g., Hall et al., 1991) or by sediment reworking by deposit feeders (e.g., Nowell et al., 1984). The formation of natural depressions may impact infaunal organisms through disturbance and removal of resident organisms and by the subsequent modification of near-bottom flow. These experiments suggest that fine-scale

hydrodynamics influence the settlement of larvae in soft-sediment habitats and that encounter with a suitable substrate may depend on near-bottom flow. This does not, however, imply that active habitat selection (e.g., Butman et al., 1988b; Butman & Grassle, 1992; Grassle et al., 1992a,b; Snelgrove et al., 1993), post-settlement processes (e.g., Luckenbach, 1984) and species interactions (e.g., Wilson, 1983) are not important. The complex pattern of animal-sediment relations (e.g. Gray, 1974; Rhoads, 1974) is likely a product of all of these factors acting in concert, and the relative importance of each factor under different circumstances is unlikely to emerge without extensive, continuing experimentation.

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# Chapter 4

## Potential Flow Artifacts Associated with Benthic Experimental Gear:

## Deep-Sea Mudbox Examples

This chapter was written to be submitted to Journal of Marine Research with co-authors C.A. Butman and J.F. Grassle

## Abstract

In response to the growing recognition of the role that near-bed hydrodynamics may have on benthic processes such as larval distribution, flume simulation experiments were conducted to document fine-scale flow patterns over several different types of colonization mudbox that have been used to estimate colonization rates of deep-sea organisms. In previous studies, these trays were filled with natural sediments and placed *in situ* to observe how timing, larval supply and sediment composition may effect larval settlement rates, however, little consideration was given to the potential hydrodynamic bias that the mudbox structures may have caused. Detailed velocity profiles were collected above two types of Free Vehicle mudboxes that could be deployed and recovered from a surface ship. One of these ("Old Free Vehicle") was designed with minimal regard for potential hydrodynamic bias and the other ("New Free Vehicle") was designed specifically to minimize flow disturbances and maintain realistic boundary layer flow. Similarly, profiles were collected above two smaller types of mudbox that were designed to be deployed by submersible. Again, one type of tray ("Single Tray Mudbox") was designed with minimal regard for hydrodynamic bias and the other ("Flush Sediment Tray") was designed to be placed flush with the ocean bottom, thus minimizing flow disturbance. Simulations indicated that structures such as the Old Free Vehicle and the Single Tray Mudbox create considerable hydrodynamic disturbance, and the flows over the sediment surface are very different from that predicted for natural environments. Accelerated flow speeds, growing secondary boundary layers and eddy

formation were observed over the sediment surface, and flow was constantly changing as it moved across the contained sediment. Alternative approaches designed to eliminate flow disturbance were successful in reducing or eliminating these artifacts. The New Free Vehicle was designed to sit on the sediment surface but create a gentle flow transition between the ambient sediment and the contained sediment. Flow over the sediment surface in this type of free vehicle did not change with increased distance downstream, and velocity profiles over the sediment surface were very similar to those in the open flume channel and those predicted for a natural habitat. Eddy formation and other major flow disturbances were not observed. Another type of tray which could be placed flush with the sediment by submersible (Flush Sediment Tray) was equally successful in achieving its design goals. Flow over the sediment surface was again very similar to that predicted for natural environments and eddy formation and other forms of disturbance were not noted, even in a simulation where the tray was placed in the flume with part of the tray deliberately exposed above the flume bottom. Although these experiments were motivated by concern over the potential effects of hydrodynamic disturbance in studying benthic recruitment processes, the same sorts of concerns and design considerations are relevant to other areas of marine science where sampling gear may cause hydrodynamic disturbance. Careful design of instrument components can reduce potential flow disturbances that may bias data collections and obscure data interpretation.

## I. Introduction

A major limitation in designing and deploying sampling gear in marine environments is the difficultly in avoiding hydrodynamic disturbance, particularly where sampling is integrated over time. Flow disturbance occurs because any object that blocks flow will alter flow streamlines in some way, and although it is possible to minimize this effect, instrumentation is often designed with little regard for this potential bias. Flow disturbance can affect processes in the water column as well as those on the bottom, however, the emphasis of this study is on hydrodynamics associated with benthic environments, particularly the deep sea.

Hydrodynamics may influence benthic environments in many different ways, including regulation of nutrient and oxygen flux, transport of detritus and other food sources for living organisms, physical forcing on structures extending above the sea bed, sediment deposition and erosion as well as sorting, and supply and redistribution of larvae and organisms (e.g., reviews of Nowell and Jumars, 1984; Jumars and Nowell, 1984; Butman, 1987). Although this study was motivated by the increasing evidence that near-bottom flows influence larval settlement (e.g., Butman, 1987), documentation of flow bias around instruments has direct applications to many other biological and non-biological processes and the data presented here have applications outside the field of benthic ecology.

There is good reason to suspect that near-bed hydrodynamics directly influence larval settlement. Many planktonic larvae are relatively poor swimmers, and in natural

flow conditions they may encounter flows that exceed their maximum swimming speeds at distances of only a few millimeters above the bottom (Butman, 1986a). Studies conducted in the field (e.g., Eckman, 1979, 1983; Butman, 1989) and under controlled flume conditions (Pawlik *et al.*, 1991; Butman and Grassle, 1992; Snelgrove *et al.*, 1993) indicate that relatively subtle flow differences may influence where larvae settle.

Accurate documentation of larval settlement and recruitment is still very much in a developmental stage, because studies have been plagued by potential hydrodynamic bias. In shallow, subtidal habitats, the relatively high and variable flow over structures raised above the seabed generally result in trapping artifacts (e.g., Butman, 1986b, 1989), making data interpretation difficult. Comparable data have not been collected explicitly for deep-sea environments, however, similar artifacts may be expected.

Several researchers have circumvented the problem of hydrodynamic bias in colonization studies by placing defaunated sediments flush with the seafloor to document timing, flow effects, and species interactions of settling larvae (e.g., Eckman, 1983; Gallagher *et al.*, 1983). This has resulted in experiments where data interpretation is fairly clear. A similar approach has been used in the deep sea, where submersibles have been used to place small colonization trays flush with the ocean bottom (e.g., Snelgrove *et al.*, 1992). These trays were designed in response to criticism of previous deep-sea colonization studies (e.g., Smith, 1985), where rectangular boxes filled with defaunated sediment ("mudboxes") were placed directly on the seabed to allow colonization over various periods of time (e.g., Grassle *et al.*, 1977; Desbruyères *et al.*, 1980; Levin and Smith, 1984; Grassle and Morse-Porteous, 1987). Unfortunately, submersibles are not

always a feasible approach to deep-water colonization studies because of the cost and time investment involved. As a result, free-vehicle arrays have been used in several deep-sea studies (e.g., Smith *et al.*, 1979; Desbruyères *et al.*, 1980; Levin and Smith, 1984). Free vehicles are structures designed to be deployed and recovered by a surface ship, and thus have the flexibility to be deployed at virtually any oceanographic location at a relatively low cost.

Mudboxes can be an excellent diagnostic tool for understanding basic ecological processes that occur in the deep sea. Mudbox sediments may be manipulated to test specific *a priori* hypotheses on processes structuring deep-sea recruitment and species coexistence (e.g., Desbruyères *et al.*, 1985; Grassle and Morse-Porteous, 1987; Snelgrove *et al.*, 1992). However, the increasing awareness that small-scale hydrodynamic processes may play a major role in larval recruitment suggests that any structure protruding above the bottom potentially could interfere with or be subjected to flows very different from the natural near-bed hydrodynamic regime. Thus, collections of animals in mudboxes may be biased by the unusual flow parameters (e.g., changes in current velocity or shear stress) generated by the mudbox itself. These parameters could be markedly different from those in the adjacent natural bottom.

The objective of this study is to use flume simulations to document the types of flows that might be expected to occur over mudbox sediments elevated above the ocean floor compared with that over the ambient sea floor, to identify specific hydrodynamic effects that might be expected to influence colonization of mudbox sediments, and offer alternative designs to minimize or eliminate these effects. Although our emphasis is on

mudboxes, the same flow considerations apply to any sampling instrument that protrudes above the bottom and remains *in situ* over a significant period of time. For example, respirometer chambers (e.g., Smith, 1978) and *in situ* core incubations (e.g. Wirsen and Jannasch, 1986) are subject to similar flow effects. Thus, the flow disturbances documented here are likely to occur in association with any similar structure deployed in a marine environment, given that the flow conditions created in the flume simulations were designed to mimic those typical of many natural situations.

*a. Boundary Layer Flow*

As a fluid moves across a solid boundary such as the sea floor, the boundary exerts a retarding force against the fluid motion. This produces a region of velocity shear referred to as the "boundary layer", where velocity directly at the sediment-water interface is zero, and increases with increasing distance above the bottom to some point where the bottom has minimal influence on the flow. This point roughly corresponds to the top of the boundary layer (Fig. 1a)., and above this point, for steady, barotropic flow, there is no vertical shear in the flow due to the bottom. Above this point is the "potential" or "frictionless" region, which is characterized by a horizontal "mean-stream" flow velocity (U) that does not change with increasing distance above the bottom in the absence of other flow effects internal to the water column.

The thickness of the benthic boundary layer may vary from millimeters to tens of meters, and can be measured directly through a series of velocity measurements or in some cases may be calculated from a limited set of measurements and theory. The

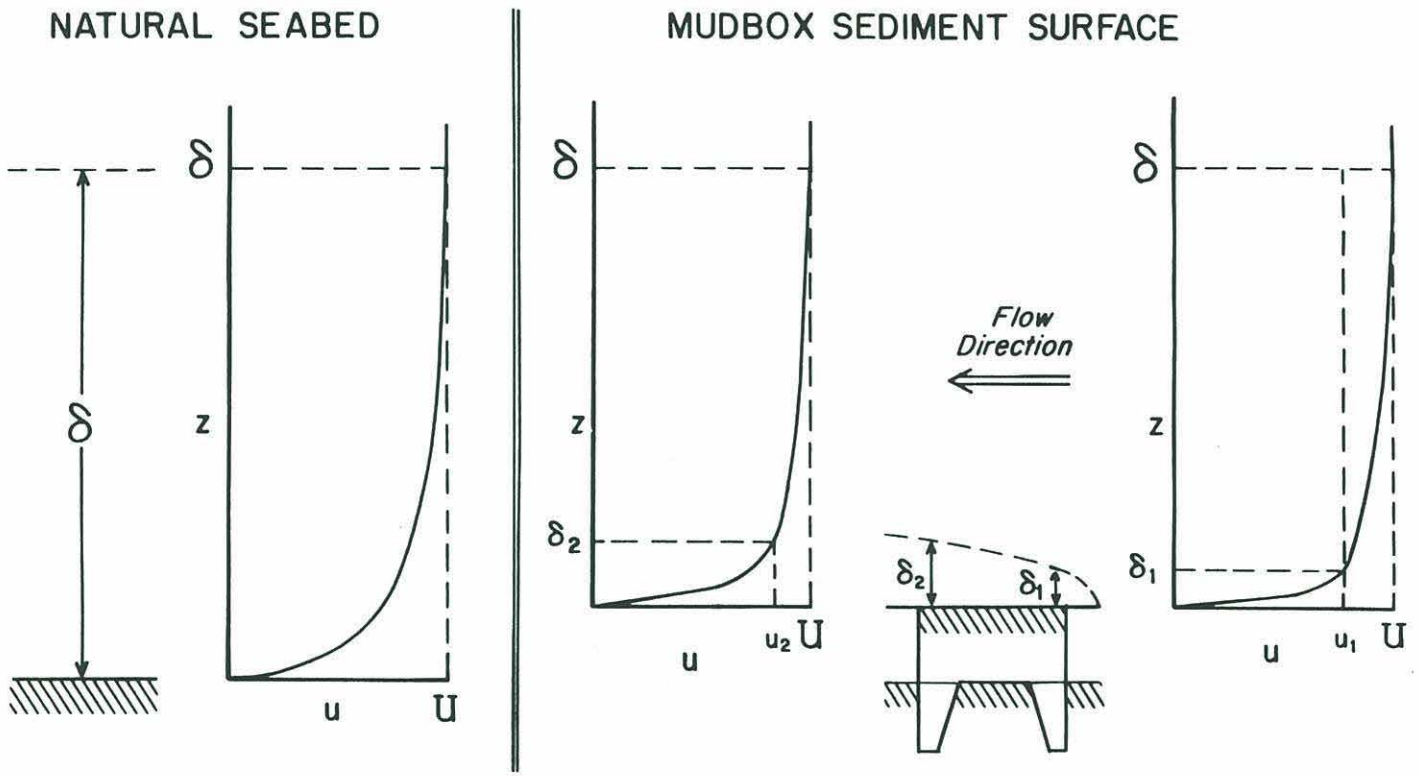


Figure 1. Diagram showing a natural bottom boundary layer profile and how the mudbox structure intercepts this profile. Also shown is the boundary layer that attaches to the leading edge of the mudbox structure and grows downstream; as the boundary layer thickens downstream, the shear near the mudbox sediment surface decreases.

thickness will depend on flow and fluid properties (e.g., the boundary shear stress $u_*$) and on the period of time over which the boundary layer has developed. In the ocean, the natural boundary layer that forms above bottom sediments in unsteady flows generated by waves and tides has a thickness of $\delta = \kappa u_* / \sigma$ where $\kappa$ is von Karman's constant of 0.4 and $\sigma$ is the forcing frequency of the flow (e.g., Grant and Madsen, 1986). The shape of the profile varies depending on flow properties (e.g., the flow Reynolds number, the background turbulence, and accelerations), fluid properties (e.g., temperature, salinity or suspended sediment induced stratification), and boundary characteristics (e.g., bed roughness, sediment cohesion).

Theoretically, the benthic boundary layer could be laminar or turbulent, depending on the relative importance of viscous as opposed to inertial forces. Relative importance of the forces is characterized by the flow Reynolds number, $Re_f = L U / \nu$ where L = characteristic length scale for the flow, U = free-stream velocity and $\nu$ = kinematic viscosity of the fluid. Laminar boundary layers occur at low $Re_f$, where turbulent fluctuations (inertial forces) are relatively unimportant. Laminar boundary layers have pronounced stream-wise stability, meaning that any disturbance to the layer will be quickly dissipated by viscosity. Thus, only horizontal velocities are present in laminar flow. Turbulent boundary layers occur at high $Re_f$. In this case, velocities have both a mean and a fluctuating component; fluctuations are a result of turbulent eddies that have velocity components in all directions. Mass and momentum are transferred within the boundary layer because of these fluctuations. The turbulence is produced by vertical shear and Reynolds stress resulting from the presence of the

boundary.

Although $Re_f$ is a good predictor of laminar or turbulent boundary layers for flows over smooth plates, other factors come into play in ocean flows travelling over sediments or bumpy seabeds. Turbulence may be generated in the flow by a source away from the bed (e.g., breaking waves) or at the sediment-water interface by a flow disturbance on the bottom. Because this turbulence is such a pervasive feature of the forcing function (see Yaglom, 1979), laminar boundaries are rare in the ocean. For turbulent flows, the roughness Reynolds number $Re_* = u_* k_b / \nu$ (where $k_b$ = the hydrodynamic roughness scale), is a better predictor of the characteristics of the bottom boundary layer.

Turbulent boundary layers may be classified as smooth, rough, or transitional (e.g., Schlichting, 1979), depending on the roughness Reynolds number of the flow. Over hydrodynamically smooth bottoms, very close to the sediment/water interface, viscous forces dominate the flow. At relatively low $Re_*$, a pronounced viscous sublayer may form. This sublayer has characteristics of laminar boundary layers, but it is relatively small compared to the total boundary layer thickness. Over hydrodynamically rough bottoms, viscosity still acts at the sediment/water interface, but a distinct sublayer does not form, and eddies penetrate within millimeters of the bed. Therefore, in rough-turbulent flow, the velocity structure very close to the bed is complicated and poorly understood (see Schlichting, 1979). For intermediate $Re_*$, transitional flow occurs with characteristics intermediate between smooth and rough turbulent. For open-channel or geophysical flows, boundary layer characteristics are known to be smooth turbulent for

$Re_* < 3.5$ and rough turbulent for $Re_* > 100$ (see review in Nowell and Jumars, 1984).

Based on empirical studies and scaling arguments (Clauser, 1956), turbulent boundary layers in laboratory flow may be divided into three regions (see Fig. 1a). At the boundary/water interface, in the viscous sublayer (for smooth turbulent flows), velocity varies linearly with distance from the boundary according to $u / u_* = u_* z / \nu$, the scaling parameters for this region of flow. The outermost region (i.e. furthest from the bed) is referred to as the log-defect layer because the defect velocity $( U - u /u_*$, is logarithmically related to $z / \delta$. Between these two layers (and overlapping with the lower portion of the log-defect layer), is the log layer, which is the major feature of steady, uniform flows. The velocity profile in the log layer is described by the formula where B = the empirically defined constant of integration. For smooth turbulent flows,

$$\frac{u}{u_*} = \frac{1}{\kappa} \ln \frac{z}{k_b} + B$$

the shape of the velocity profile in the log layer depends on $u_*$. For fully developed rough turbulent flow, the velocity profile depends on $u_*$ and also bed geometry. From empirical studies of smooth turbulent pipe flow (Schlichting, 1979), the lower limit of the log layer is approximately $11.6 \nu / u_*$ and the upper limit of the viscous sublayer is $5.0 \nu / u_*$. Between these heights is a complicated wake layer that cannot be described simply. In channels and geophysical boundary layers, this region may be larger (Nowell, 1983; Grant and Madsen, 1986).

A primary goal of flume studies is to match the shear velocity in the flume to

natural shear velocities. Because log-layer characteristics determine shear velocity, flows may be reproduced in the flume by matching velocities in a number of logarithmically spaced points in the log layer to those that occur naturally.

*b. The Mudbox Case*

We here compare flow over a free vehicle (Fig. 2, hereafter referred to as "Old Free Vehicle") and a submersible-deployed mudbox (Fig. 3, hereafter referred to as "Single Tray Mudbox") that were designed with minimal regard for potential flow biases, with flow over a free vehicle (Fig. 4, hereafter referred to as "New Free Vehicle") and submersible-deployed sediment tray (Fig. 5, hereafter referred to as "Flush Sediment Tray") specifically designed to minimize potential hydrodynamic bias. The older tray designs sit on the sediment surface and penetrate inside the boundary layer that forms over the natural bottom sediments (Fig. 1b). The sediment surface within a mudbox also presents a boundary to the flow, so that an additional boundary layer forms above the mudbox sediments. Thus, flow velocities over these structures result from a boundary layer within a boundary layer, and are very different from flows over the natural bottom. This problem may be circumvented in either of two ways. The New Free Vehicle was designed so that separation of the natural boundary layer would not occur, and the boundary layer over the sediment would be comparable to that over the natural bottom. The Sediment Tray, however, was designed to be placed flush with the bottom, so that flow would not be altered by the presence of the tray. In this study, we are seeking to compare velocity characteristics within the natural bottom boundary layer

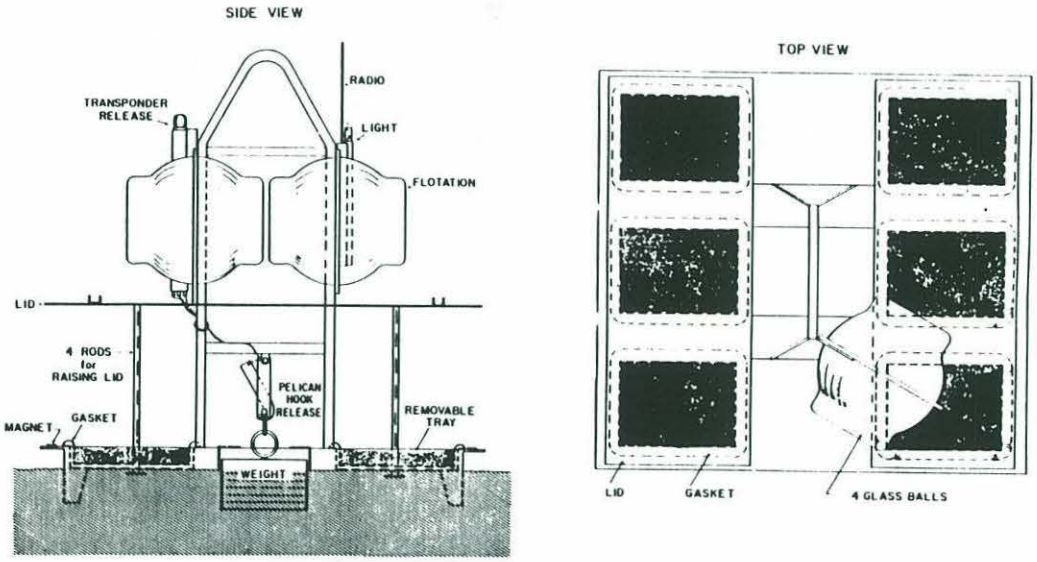


Figure 2. Diagrams of the Old Free Vehicle showing a side view (left) and a top view (right). The free vehicle consists of a 1.52 m by 1.42 m rectangular fiberglass frame to hole the six removable polyethylene mudbox trays (30 cm by 40 cm by 7.5 cm deep, a fiberglass lid to cover the trays during transport, and an aluminum support structure to which flotation (glass spheres with polyethylene jackets, the transponder release, the radio beacon, the strobe light, signal flag, and the pelican-hook release are attached. When the structure is lifted off the bottom, it rises to meet the lid, creating a tight seal; when the structure is placed on the seabed, the lid is raised 43 cm above the mudbox sediments via the 4 support rods. To create negative buoyancy, steel plates are attached to a ring beneath the center of the mudbox frame. The ring attaches to the pelican-hook release and, upon an acoustic command from the surface vessel, a burn-wire holding the pelican hook vertical is electrically corroded. The nichrome burn-wire is completely covered with shrink tubing to insulate it from seawater, except for one small notch where the pelican hook is held against the vehicle frame. The burned wire releases the hook so it falls down horizontally and the ring slides out. The weights are then released from the frame, the mudbox structure rises to meet the lid (which seals tightly via silicone rubber gaskets around each tray and magnets all around the perimeter of the lid) and the entire structure floats to the surface. The aluminum frame is about 1 m high (from the trays to the horizontal cross bar) and has a loop on top to allow deployment and retrieval using the ship's crane.

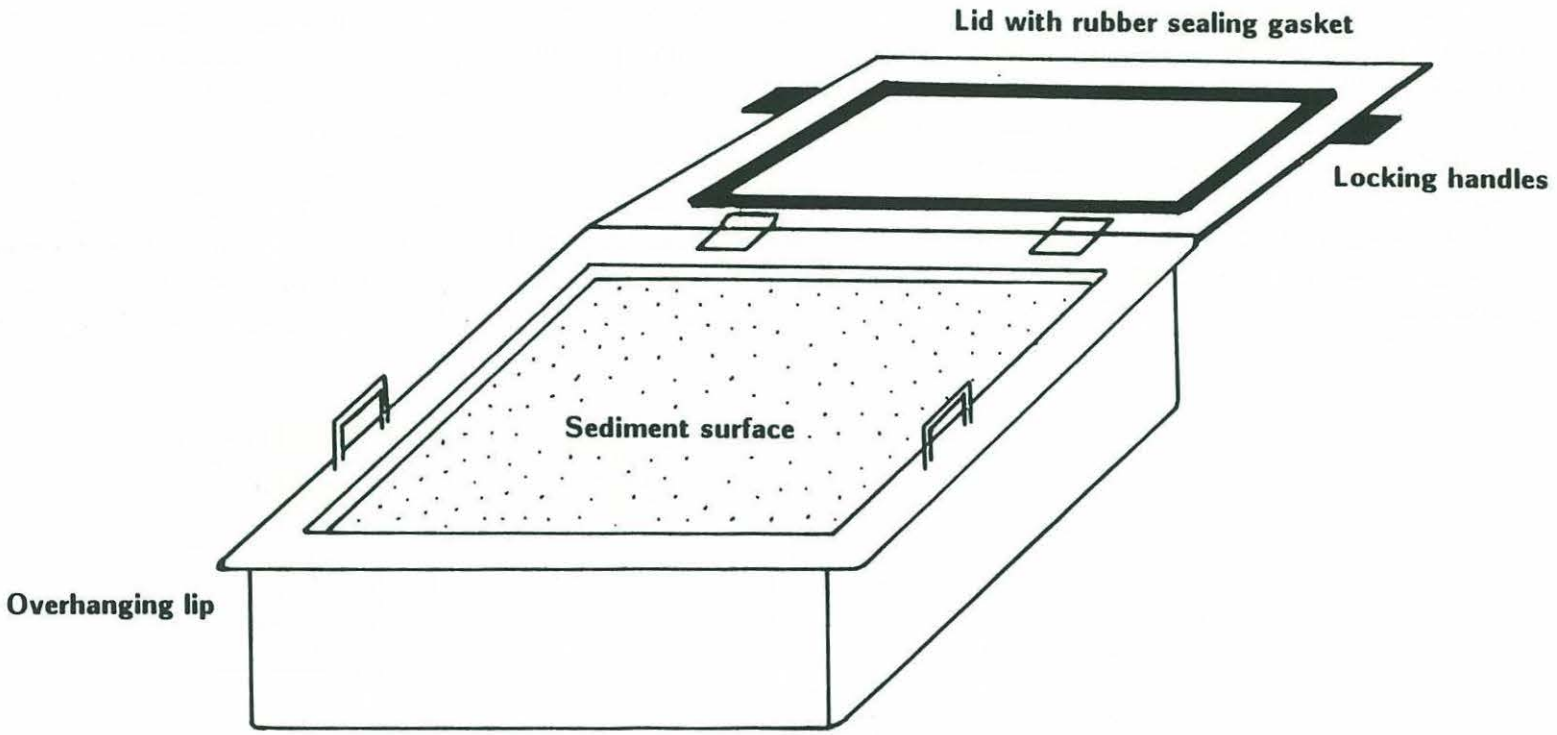


Figure 3. Diagram of the Single Tray Mudbox. The fiberglass tray (50 cm by 50 cm by 12.7 cm deep) is sealed by a lid during transport to and from the surface by submersible (or diver). A rubber gasket forms a tight seal between the lip of the trap and the lid. A t-handle on the other face of the lid is rotated to move the locking handles, which may slide under the loops on the trap lip to lock and form a tight seal.

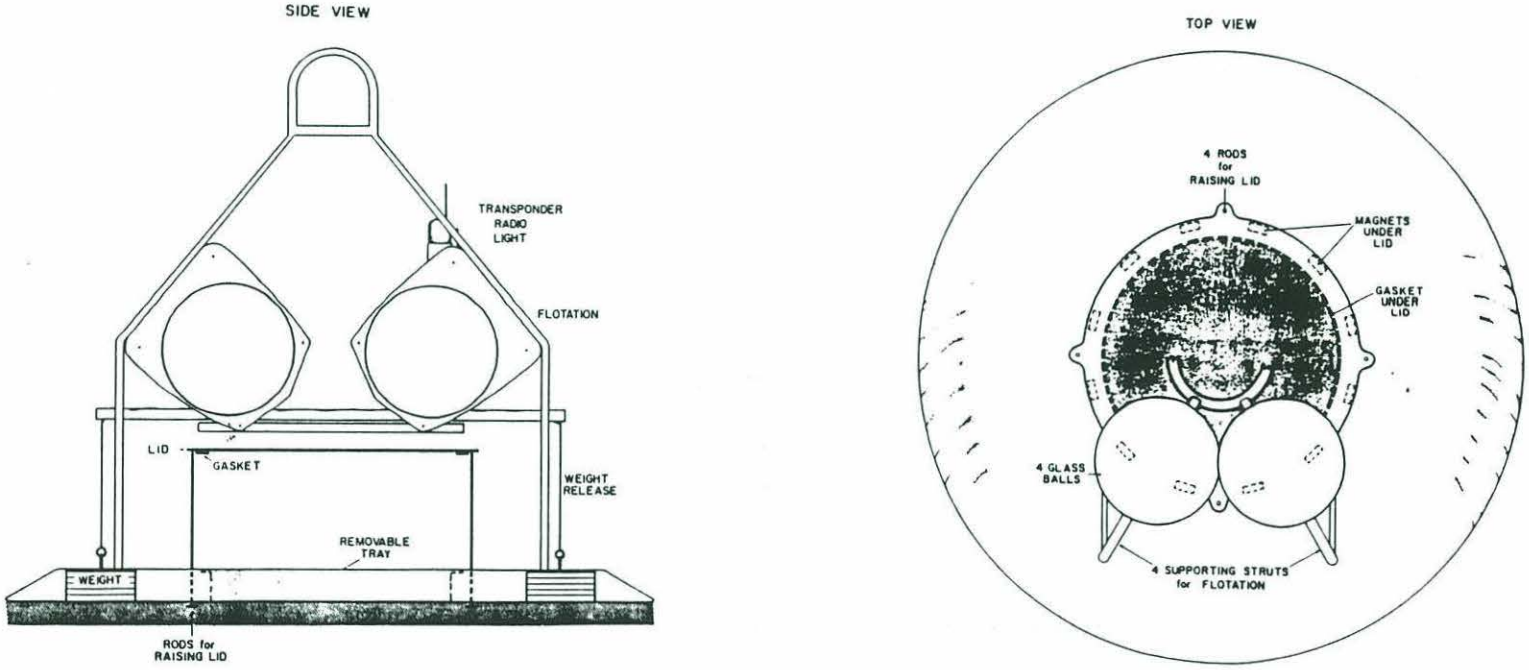


Figure 4. Diagrams of the New Free Vehicle, showing a side view (left) and a top view (right). The lid opening and closing mechanism and the release mechanism are identical to those described for the Old Free Vehicle (see caption of Fig. 2).

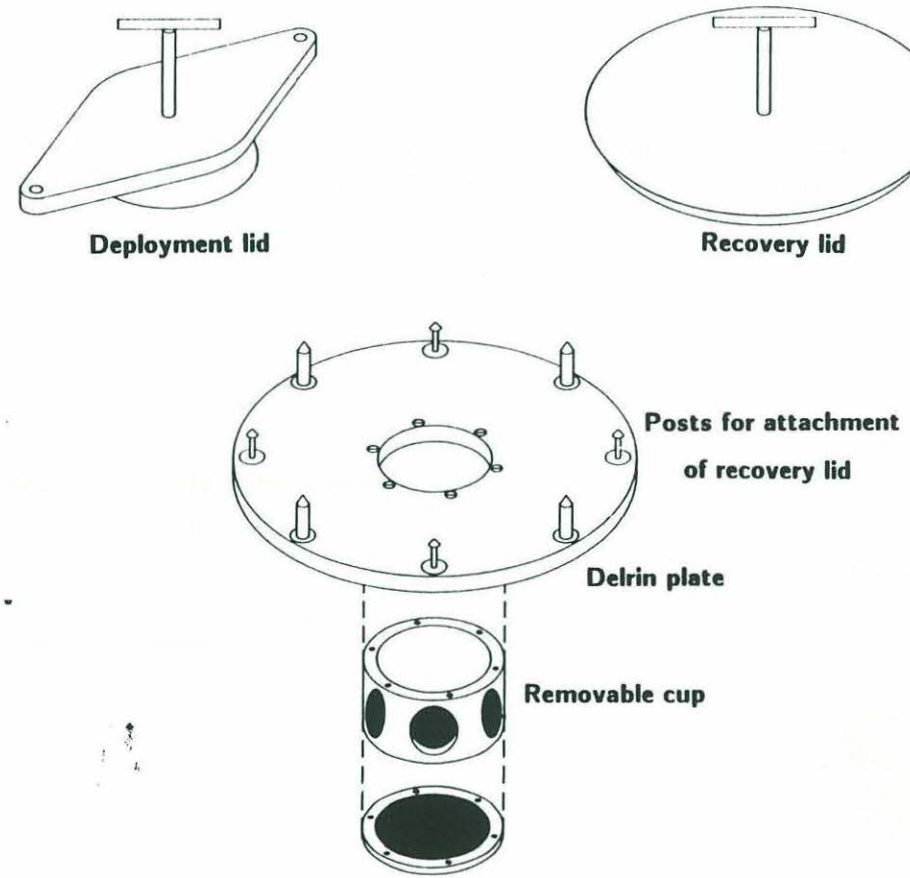


Figure 5. Diagram of the Flush Sediment Tray showing separated components. The central cup is filled with sediment and the deployment lid is attached to the tray with cotter pins attached to a monkey fist, sealing the sediment in the tray during transport to the bottom. The submersible then excavates an area of the approximate dimensions of the tray and then moves the tray around in the depression until the tray is flush. When sediment clears, the lid is removed. The recovery lid is attached by pushing it down from above, forcing the locking pins at the periphery of the tray to bend back. When the lid is pushed down far enough, the pins snap back to the vertical and lock it in place. Sealing gaskets in both lids prevent sediment leakage.

with velocity characteristics observed over the different designs of mudboxes.

## II. Materials and Methods

### *a. Characterization of Natural Flow*

In order to evaluate flow over free vehicles and colonization trays, it was necessary to recreate flow conditions approximating those that might be expected to occur naturally. Given that many of the deep-sea colonization experiments have been conducted on the Atlantic Continental Slope and Rise off the New Jersey coast, flow conditions from this area were mimicked. The Flush Sediment Tray has been deployed south of St. Croix, U.S.V.I. (Snelgrove *et al.*, 1992) and the flow conditions that occur there are roughly comparable to those that occur on the New Jersey Slope. Thus, similar flow conditions were reproduced for each of the mudboxes tested.

Profiles of horizontal current speed within the log layer can be calculated for a site given the following assumptions. (1) There is quasi-steady, uniform, neutrally stratified flow over the bed. (2) The bed is uniform over large horizontal distances, relative to the height above the bed where velocities are calculated. (3) Bottom roughness is small compared with boundary-layer thickness. In addition to these assumptions, information must be available on velocities occurring at some height above the bottom within the log layer and on bottom roughness characteristics. Although unsteady and non-uniform flows make bottom flow difficult to predict (e.g., see Grant and Madsen, 1986), the assumptions described above are met, at least periodically, at

the mudbox deployment sites on the Atlantic Continental Slope and Rise (or St. Croix), and deviations from these assumptions are not critical for the first-order approach of this study.

Given the range of near-bed flow speeds and bottom types expected at the study sites, values of $Re_*$ fall in the smooth-turbulent range. The log-layer equation has the specific form

$$\frac{u}{u_*} = \frac{1}{\kappa}\left(\frac{\ln(zu_*)}{\nu}\right) + 5.5$$

for smooth-turbulent pipe flows (Schlichting, 1979), but the constant differs for channel flows and geophysical flows. The smooth-turbulent profile was calculated for $\nu = 0.01$ $cm^2\ s^{-1}$ and for u = 15 cm at z = 500 cm. This velocity falls within the range of flows expected to occur at these and other deep-sea sites (Grassle and Morse-Porteous, 1987; Mullineaux and Butman, 1990; Butman, pers. comm.); although faster and slower flows do occur in these habitats, simulations were done under median rather than extreme flow conditions.

*b. The Free Vehicles*

Four different mudbox types were tested in the flume, including two free vehicles and two submersible-deployed trays. The Old Free Vehicle (Fig. 2) consists of a square fiberglass frame (1.52 m by 1.42 m) containing six identical polyethylene trays (30 cm by 40 cm by 7.5 cm deep) that are filled with defaunated sediment. A fiberglass lid

covers the trays and retains sediment during transport to and from the bottom; an aluminum support structure bears the flotation, the transponder release, and the pelican hook release. The frame is raised on feet such that the tray sediments are approximately 10 cm above the bottom on a hard surface, but sink slightly into a natural muddy bottom. When the free vehicle rests on the bed, the lid is raised 43 cm above the top of the trays so that it does not interfere with flow over the sediment surface. Steel plates attached to the underside of the center of the frame make the vehicle negatively buoyant; upon acoustic release, the plates are dropped and the vehicle rises from the bottom and meets with the lid before continuing on up to the surface for recovery. A square, rubber gasket (1 cm x 1 cm) spans the lip of each of the trays and, with the aid of magnets around the lid perimeter, seals the trays with the lid during deployment and recovery.

The New Free Vehicle, which was designed to reduce flow disturbance (see Discussion), consists of a round sediment tray (80 cm in diameter) located at the center of a large, radially symmetrical smooth flat disc (224 cm diameter) which slopes gently to the seabed at its perimeter (Fig. 4). The central sediment tray is filled with defaunated sediment so that it is flush with the disc. The disc is made from molded ABS plastic (0.64 cm thick), and support structures underneath the disc hold the structure rigid. A weighting and acoustic release mechanism similar to that used in the Old Free Vehicle design are also employed here, except that the weights, release mechanism and floatation are in the periphery of the vehicle. As in the Old Free Vehicle design, the tray floats up to meet the lid; a gasket and magnets seal the lid

against the disc during deployment and recovery. The sediment surface is approximately 10 cm above the natural seabed.

*c. The Colonization Trays*

A smaller type of colonization tray, the Single Tray Mudbox (Fig. 3), is deployed by submersible and has been used in several deep-sea studies (e.g., Grassle, 1977; Grassle and Morse-Porteous, 1987). A thin lip (width 3 cm) extends around the periphery of a single fiberglass tray (12.7 cm in height, 50 cm in width and 50 cm in length), which is filled to within 1 cm of the lip with defaunated sediment. A PVC lid is attached with a hinge to one side, and flips down over the tray to seal it during transport to and from the bottom. A sealing gasket similar to that described above is attached to the lid rather than to the box itself. Because some deep-sea experiments were conducted with a screened version of this mudbox (Grassle and Morse-Porteous, 1987), flume simulations were also performed with 2-mm Nytex screen fastened to the top of the box parallel to the sediment surface. The screening material was not rigid, and formed gentle contours which occasionally touched the sediment surface. For flume experiments, the lid was oriented downstream of the flow.

A second type of submersible-deployed colonization tray (Fig. 5) was designed to eliminate hydrodynamic bias (Snelgrove *et al.*, 1992). Briefly, the Flush Sediment Tray consists of a central cup (11.2 cm diameter) that is fastened to a Delrin plate with a central opening of the same diameter. This results in a central well 10 cm deep that is filled with prefrozen sediment, sealed with a lid, and carried to the bottom by

submersible. It is then placed flush with the seafloor and the sealing lid is removed. Posts at the periphery of the tray allow attachment of deployment and recovery lids and cause minor flow disruption, but they are located sufficiently far away from the sediment cup in the center of they tray so that flow recovers before it passes over the sediment. The tray is described in more detail in Snelgrove *et al.* (1992).

*c. The Flume*

Experiments were performed in the 17-Meter Flume located at the Coastal Research Laboratory of the Woods Hole Oceanographic Institution (Butman and Chapman, 1989; Trowbridge *et al.*, 1989). The flume is filled with recirculating, temperature-controlled sea or fresh water, and water depth and velocity may be varied to produce a variety of flows. Velocity measurements are made with a laser-Doppler velocimeter (LDV), which allows non-intrusive flow measurements where the measurement volume in less than a square millimeter.

The channel width of the flume is 60.5 cm, which made it necessary to modify the free vehicles. Thus, 60-cm-wide model sections were made of the free vehicles for flow characterization in the flume. In the case of the Old Free Vehicle, the section was taken parallel to the longest dimension of the individual trays. Thus, a section of the free vehicle containing two complete trays with their long axis parallel to the flow was placed in the flume (see Fig. 2). For the New Free Vehicle, a 60-cm wide section was built from PVC (polyvinyl chloride) to mimic the center of the tray, encompassing most of the central sediment area (see Fig. 4). The sloping perimeter of the tray was

carefully reproduced for the upstream edge: however, the downstream end of the mimic was terminated just behind the sediment area because the downstream flow in this flume simulation was unimportant. Under natural conditions where flow direction may change, however, the symmetry of the design is important.

For both free-vehicle designs, the structures completely blocked the flow in the lower 10 cm of water in the flume, creating a bluff body effect and forcing the flow over, rather than around, the mudboxes. Under natural conditions, flow could move around, as well as over, the free vehicles: therefore, it is uncertain how realistic this bluff body effect would be relative to field conditions. The problem was identical for both free vehicle designs, and other than exaggerated flow acceleration over the trays, the experiment was expected to be a realistic simulation of flow over the central portion of the structures. Allowing flow around the sides of the free vehicles in the flume would likely have created more serious flow artifacts because the morphology of the boxes would be incorrect (i.e., the occurrence of sharp edges that do not occur in the designs).

The Single Tray Mudbox was only 50 cm in width and therefore could be placed directly in the flume without any modification. However, to create a similar, bluff-body effect to the other designs and to eliminate funneling of flow along the sides of the mudbox, a thin (3 mm) PVC plate was placed at the corners of the leading edge of the mudbox. The plates were cut to fit just under the lip of the sediment tray. Thus, the bluff body effect was similar for both free vehicles as well as the Single Tray Mudbox.

A section of the flume bottom could be removed and replaced with a 50 cm x

50 cm x 50-cm deep box, which may be filled with sediment so that it is flush with the floor of the flume. The Flush Sediment Tray was placed flush with the floor of the flume, much as it would be placed on the ocean floor under ideal and poor deployments (see Fig. 13). The Flush Sediment Tray was therefore unique because it could be placed flush, or near-flush, with the flume bottom, and thus no bluff body effect occurred.

A further complication to flume simulations was the height of the free vehicles and the Single Tray Mudbox. The Single Tray Mudbox reached a height of slightly more than 12 cm from the bottom and the contained sediments were therefore approximately 11 cm above the bottom. Although the upper frame (i.e., parts of the free vehicles higher than the sediment trays) were removed to allow placement in the flume, both free vehicles, as well as their sediment surfaces, reached a height of approximately 10 cm from the bottom. It was therefore necessary to maintain a water depth of approximately 23 cm above the flume bottom to quantify flow over the structures. This water depth was maintained for all experiments, and although slight fluctuations in water level did occur, variation of only 3% or less was considered acceptable during the course of a profiling series. In instances where this criterion was not met, the experiment was terminated and the results discarded. Ideally, flume simulations should maintain a minimum width to depth ratio of at least five to avoid secondary circulation effects associated with boundary layer growth along the flume walls (Nowell and Jumars 1987). Unfortunately, it was impossible to satisfy this criterion in this flume and still quantify flow over structures as large as the mudboxes. Thus, secondary flow effects may have occurred, making cross stream measurements somewhat meaningless. The

goal of the simulation, however, was to quantify downstream changes in flow over the sediment surface, and no cross-stream comparisons were made. Several profiles were made along the flume channel in the test area before adding the mudboxes to determine whether any downstream changes in shear velocity ($u_*$) or boundary layer growth were evident; these criteria were far more important for the purposes of the study.

All of the designs were compared under a flow regime with $u_* \approx 0.40$ cm $s^{-1}$, where velocities near the water surface were approximately 10 cm $s^{-1}$ and water depth was approximately 23 cm. Although this shear velocity is slightly less than that expected to be typical of the natural environments where mudboxes have been deployed (0.49 cm $s^{-1}$, see Results), simulations were also conducted at shear velocities higher than those thought to be typical. Thus, simulations for the Old Free Vehicle and the New Free Vehicle were conducted at shear velocities of approximately 0.40 cm $s^{-1}$ (hereafter referred to as "slow flow") and 0.60 cm $s^{-1}$ (hereafter referred to as "fast flow"). These shear velocities not only encompass median velocities expected at the deep-sea sites, but also fall within the range of steady, tidal flows expected in typical shallow-water embayments (e.g., Butman, 1986a). Undoubtedly, more extreme flow conditions do occur at the site, however, the goal of the simulation was to mimic median flow. The two submersible-deployed mudboxes were tested only in the slower flow conditions; however, these designs were also tested for other potential flow artifacts. For the Single Tray Mudbox, simulations were conducted both with and without Nytex screening (2-mm square openings) that was used in field experiments to determine the potential effects of predator exclusion (Grassle and Morse-Porteous,

1987). This comparison was designed to document potential effects of screening on flow over mudboxes. In both Single Tray Mudbox simulations, the sides of the mudbox were cut away to allow profiling down to the sediment surface (i.e., ≈ 1 cm below the lip of the tray); however, the Nytex screen was not rigid and formed wavy contours. The mesh, therefore, blocked the laser beams of the LDV and made it impossible to profile below the screening close to the sediment surface. For the Sediment Tray, simulations were conducted with the tray flush with the flume bottom and also with the leading edge of the tray purposely exposed, thus simulating "good" and "poor" deployments *in situ* and making it possible to determine whether poor deployments of this type of mudbox result in hydrodynamic artifacts.

Theoretical calculations indicated that the log layer in the open flume was between approximately 0.3 and 5.0 cm above the bottom, therefore, profile points in the open channel were roughly logarithmically spaced within this region. Because flows over the mudboxes were unknown and were likely more complex than those in the open flume channel, profile points over these structures were roughly evenly spaced. In areas where more detail was desired, 15-point profiles were measured, whereas only 10 points were measured elsewhere. Profiles were taken over the mudboxes at downstream distances providing the most information on how the design influenced flow, and how the boundary layer changed over the sediment.

The sediment used in the Old Free Vehicle, New Free Vehicle and Single Tray Mudbox simulations was originally obtained from the U.S. Mid-Atlantic Slope at 2100 m. Despite slight differences in the actual heights of the mudboxes, the sediment

surface in each case was about 10 cm above the floor of the flume (11 cm for the Single Tray Mudbox). The Sediment Tray was filled with sediment from the St. Croix site where this type of tray has been used for *in situ* experiments (Snelgrove *et al.*, 1992). Although this sediment is somewhat coarser than the muddy sediment from the Mid-Atlantic slope, this roughness is buried within the viscous sublayer in smooth-turbulent flow, and therefore has no effect on shear velocity or the shape of the profile. The sediment in all of the mudboxes was situated in the same area of the test section, so that the front edges of the sediment in the respective trays were aligned at the same point along the flume channel (10.13 cm downstream from the flume entrance). Therefore, the leading edge of the new design extended 0.60 m further upstream than that of the old design. Also, because the lip of the single tray mudbox was relatively small, it did not extend quite as far upstream as the old design free vehicle (leading edges differed by 9 cm in location). These location differences were not considered important given that no major changes in flow were noted at any point along the flume within the test section prior to the addition of the mudboxes, and flow over the sediment surfaces (which were located in the same area of the flume) was the most important issue.

## III. Results

### *a. Natural Flow Conditions*

The typical flow condition estimated for the deep-sea sites is based on an

average velocity of 15 cm $s^{-1}$ at 500 cm above the bottom (the average of the two sites in Grassle and Morse-Porteous, 1987), resulting in an estimated shear velocity of 0.49 cm $s^{-1}$. Thus, flume simulations were run with shear velocities of approximately 0.40 and 0.60 cm $s^{-1}$ to bracket this estimate. The most important aspect of this calculation is that natural sediments on the bottom experience relatively modest flows beneath the viscous sublayer (< 1 cm $s^{-1}$); however, the sediment surface in the Old Free Vehicle, for example, is elevated well into the log layer where flows approaching the sediment are on-the-order-of 10 cm $s^{-1}$ (Fig. 6). Thus, the flow over mudbox sediments is very different from that over the natural sediments. The details of these flow differences are more apparent in flume simulations.

*b. Flume Flow Characterization*

To determine whether flow characteristics changed along the flume channel in the area where mudboxes were tested, measurements were made at widely-spaced intervals along the channel before mudboxes were added. Profiling was done at points along the flume channel corresponding to the location of the leading edge of the New Free Vehicle, the leading edge of the Old Free Vehicle, and a position near the furthest downstream measurement location. For slow flow (≈10 cm $s^{-1}$, $u_* = 0.42$), the shear velocities and shapes of profiles were similar at each of the areas (Fig. 7a). In fast flow (15 cm $s^{-1}$, $u_* = 0.62$), the shear velocities and shapes of profiles were again very similar (Fig. 7b). Thus, based on velocity profiles collected in the absence of mudboxes, the flow that approached each of the mudbox types was quite comparable. Other than

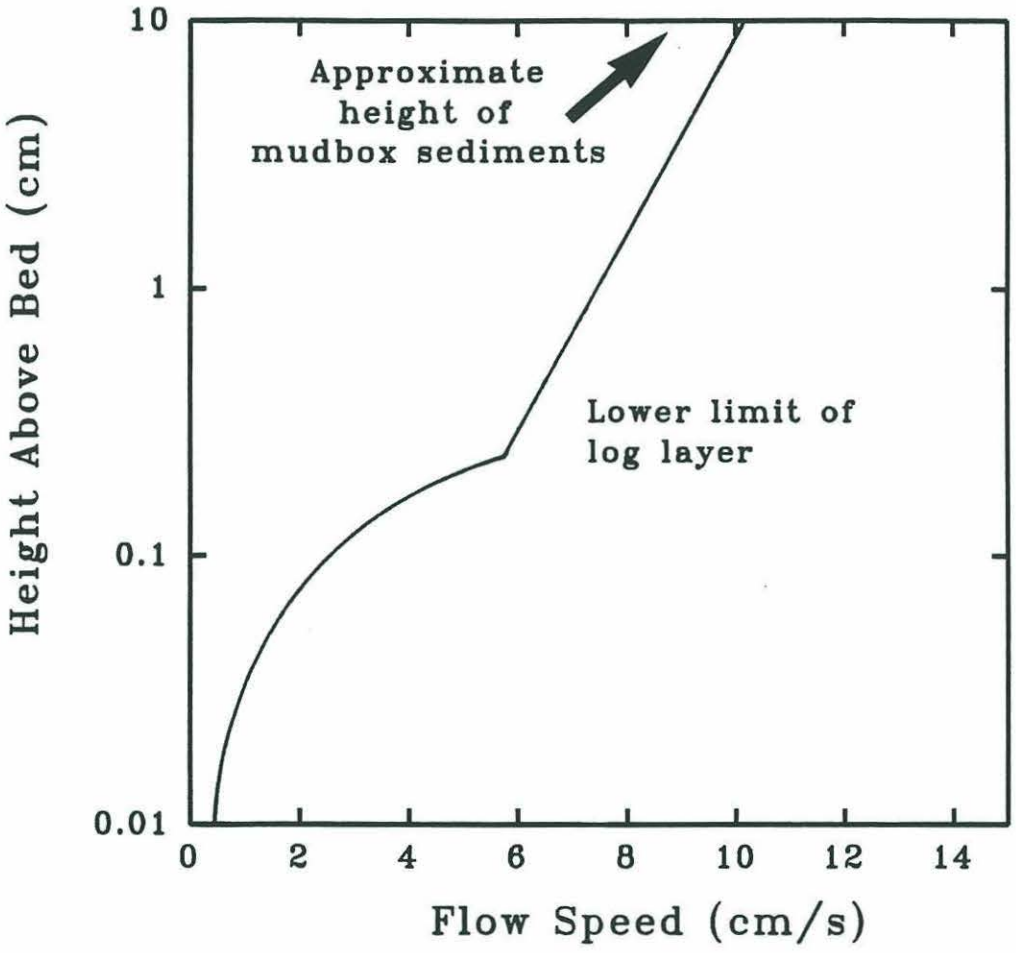


Figure 6. A smooth-turbulent velocity profile over the natural seabed, calculated using $u = 15$ cm $s^{-1}$ and $z=500$ cm. The viscous sublayer is observed between the log layer and the sediment surface, and the full boundary layer is not shown on this plot.

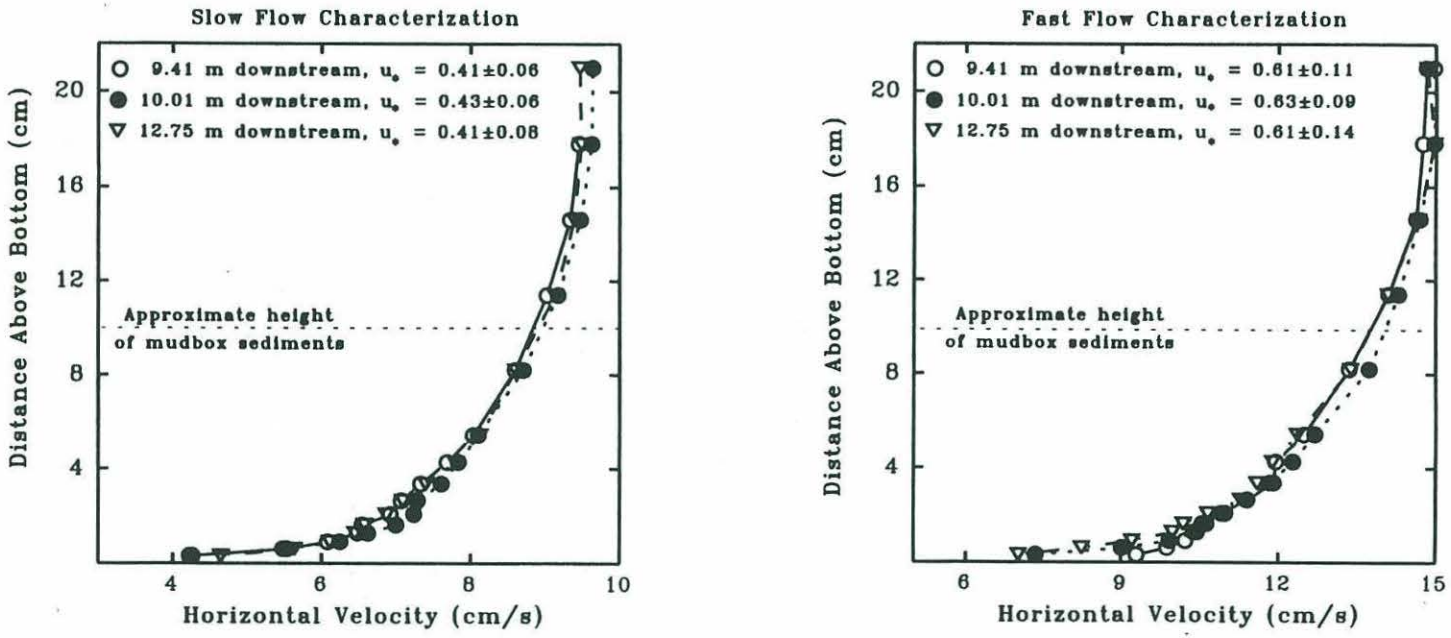


Figure 7. Velocity profiles taken at three points along the flume axis encompassing the test section where measurements over mudbox sediments were made. Shear velocities ($u_*$) were calculated using all points in the profile. 95% Confidence intervals are given for each estimate.

matching shear velocities between natural flow conditions and the flume simulation, another important aspect of the simulation is that the portion of the boundary layer crossing the sediment surface is comparable. Although the natural boundary layer in the deep sea may be quite thick (10's of meters) relative to shallow water, the flume flow is a reasonable simulation because the most critical scaling parameters, $u_*$ and $z_0$ (height where flow is effectively zero), are independent of velocity and height above bottom (e.g., Nowell and Jumars, 1987).

*c. The Free Vehicles*

In the slow-flow simulation, flow approaching the sediment tray in the Old Free Vehicle was complex (Fig. 8). Directly above the fiberglass lip at the leading edge of the tray, negative velocities were observed above the lip and positive velocities were observed with increasing distance above the lip, suggesting that an eddy formed upstream of the rubber sealing gasket. Above the sealing gasket, just downstream of the fiberglass lip, positive flow speeds were much higher than those measured in the absence of a mudbox. Just above the gasket, velocities on the order of 9 cm $s^{-1}$ were observed, much as predicted based on calculations of the natural boundary *in situ* (Fig. 6) and measurements made in the flume prior to the addition of mudboxes (Fig. 7). Several centimeters downstream from the gasket over the upstream portion of the sediment surface, negative velocities were again observed. Within one centimeter of the sediment surface, flows were negative at 4 centimeters downstream from the gasket, suggesting that an eddy (or eddies) had formed just behind the gasket. Further

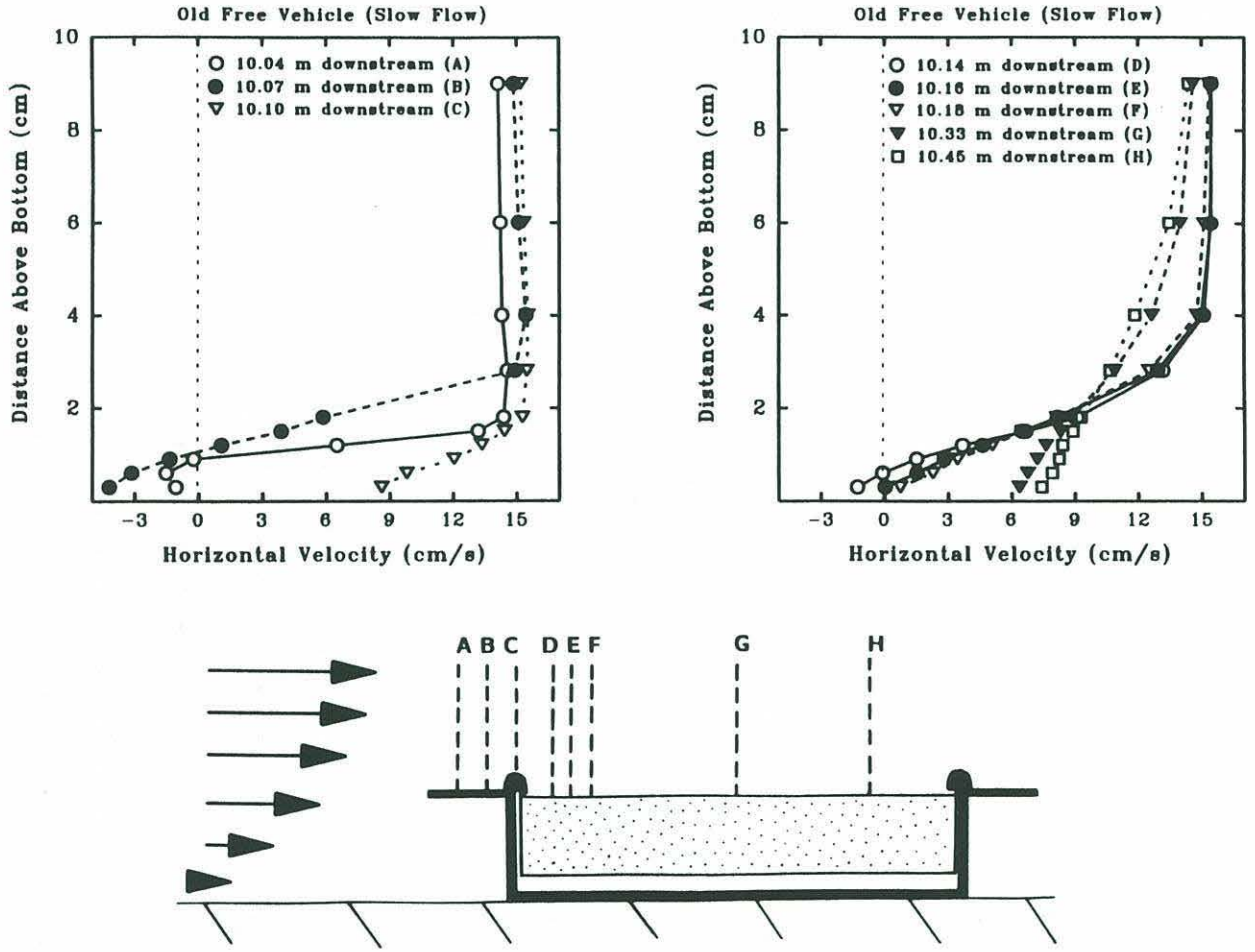


Figure 8. Velocity profiles measured at different points along the Old Free Vehicle upstream of the sediment surface (left) and directly over the sediment surface (right) for slow flow conditions (see text). Points along free vehicle where velocities were taken are summarized in the diagram beneath the plots. Profile points were roughly evenly spaced and based on 6-minute LDV measurements.

downstream, negative velocities were not observed, and a secondary boundary layer appeared to be forming over the sediment surface. This is apparent from the shifting of velocity profiles observed as flow progressed downstream; the flow characterized by relatively slow velocities close to the sediment surface and fast velocities nearer the water surface became more developed downstream and velocities close to the sediment surface become somewhat faster and flow further away from the sediment became slower. Thus, the flow across the sediment tray was constantly changing with increasing distance downstream as the boundary layer grew. The generally higher flow speeds observed over the tray compared with the open channel case is exaggerated by the bluff body effect of the mudbox in the flume, and would be less pronounced *in situ*.

Qualitatively, the same result was observed for the Old Free Vehicle in fast flow as observed in slow flow (Fig. 9). The size of the eddy formed downstream of the gasket may have been marginally larger than in slow flow, given that negative velocities were observed 6 centimeters downstream of the gasket compared with 4 centimeters in slow flow. Not surprisingly, under these flow conditions velocities were generally faster in all cases, however, the shapes of the profiles at different areas were remarkably similar in shape for slow and fast flows. Thus, the flow effects observed here may be qualitatively similar over a range of flow conditions.

In the new design, the flow transition over the sediment surface was much smoother (Fig. 10). Although the shape of the profile changed as flow moved past the leading edge of the free vehicle up onto the raised surface where the sediment was contained, boundary layer detachment was not observed. The absence of negative

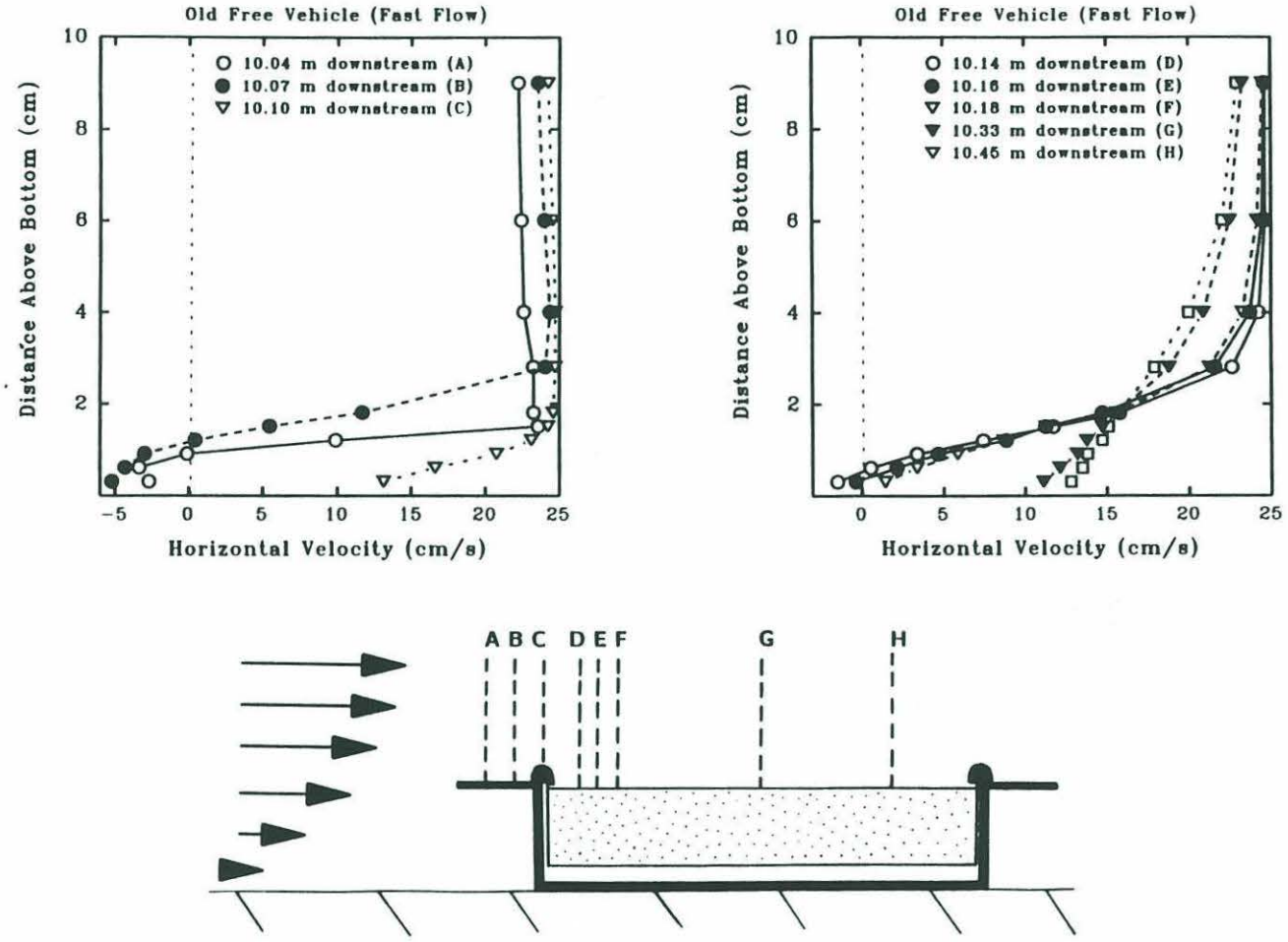


Figure 9. Velocity profiles measured at different points along the Old Free Vehicle for fast flow conditions. See caption of Figure 8.

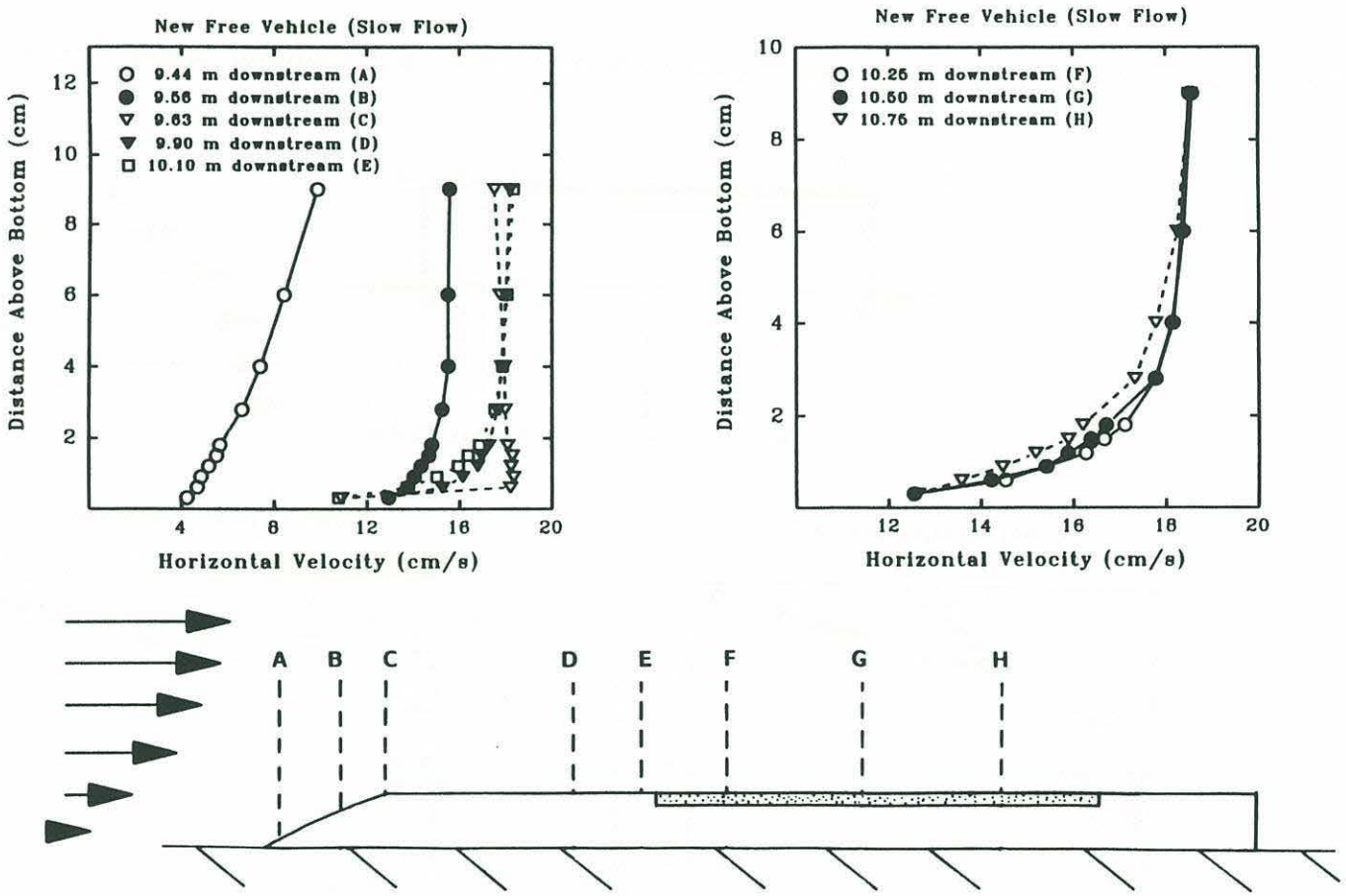


Figure 10. Velocity profiles measured at different points along the New Free Vehicle upstream of the sediment surface (left) and directly over the sediment surface (right) for slow flow conditions. Points along the free vehicle where velocity profiles were taken are summarized in the diagram beneath the plots. Profile points were roughly evenly spaced and based on 6-minute LDV measurements.

velocities downstream from the leading edge also suggests that eddies were not formed anywhere over the mudbox structure. Flow was reduced near the mudbox surface, particularly just before the crest of the leading edge (measurement c in Fig. 10). Most importantly, however, flow over the sediment surface did not change appreciably, and at least qualitatively resembled flow in the open channel case (Fig. 7). Although flow acceleration was observed relative to the open channel, this was again, in part, a function of the bluff body effect of the mudbox in the flume, and acceleration *in situ* would be expected to be substantially reduced. As with the Old Free Vehicle, velocity profiles above the New Free Vehicle under fast flow conditions were remarkably similar to those under slow flow (Fig. 11). Although flow speeds were greater, and larger acceleration was observed, the shapes of the profiles were very similar to those measured for slow flow over the New Free Vehicle. Thus, this design was fairly successful in achieving the goal of mimicking background flow conditions over the contained sediment.

In a general sense, flow over the Single Tray Mudbox was similar to that over the Old Free Vehicle (Fig. 12). Although there was no sealing gasket at the upstream edge of the Single Tray Mudbox, negative velocities indicative of eddy formation were observed just above the overhanging lip at the leading edge; evidently, the overhanging lip created complex hydrodynamic disturbance. At the upstream edge of the sediment surface, just behind the lip, negative velocities (and eddy formation) were again observed. Further downstream, profiles above the sediment surface were close to linear, and very different from characteristic boundary layer shape. Thus, a secondary

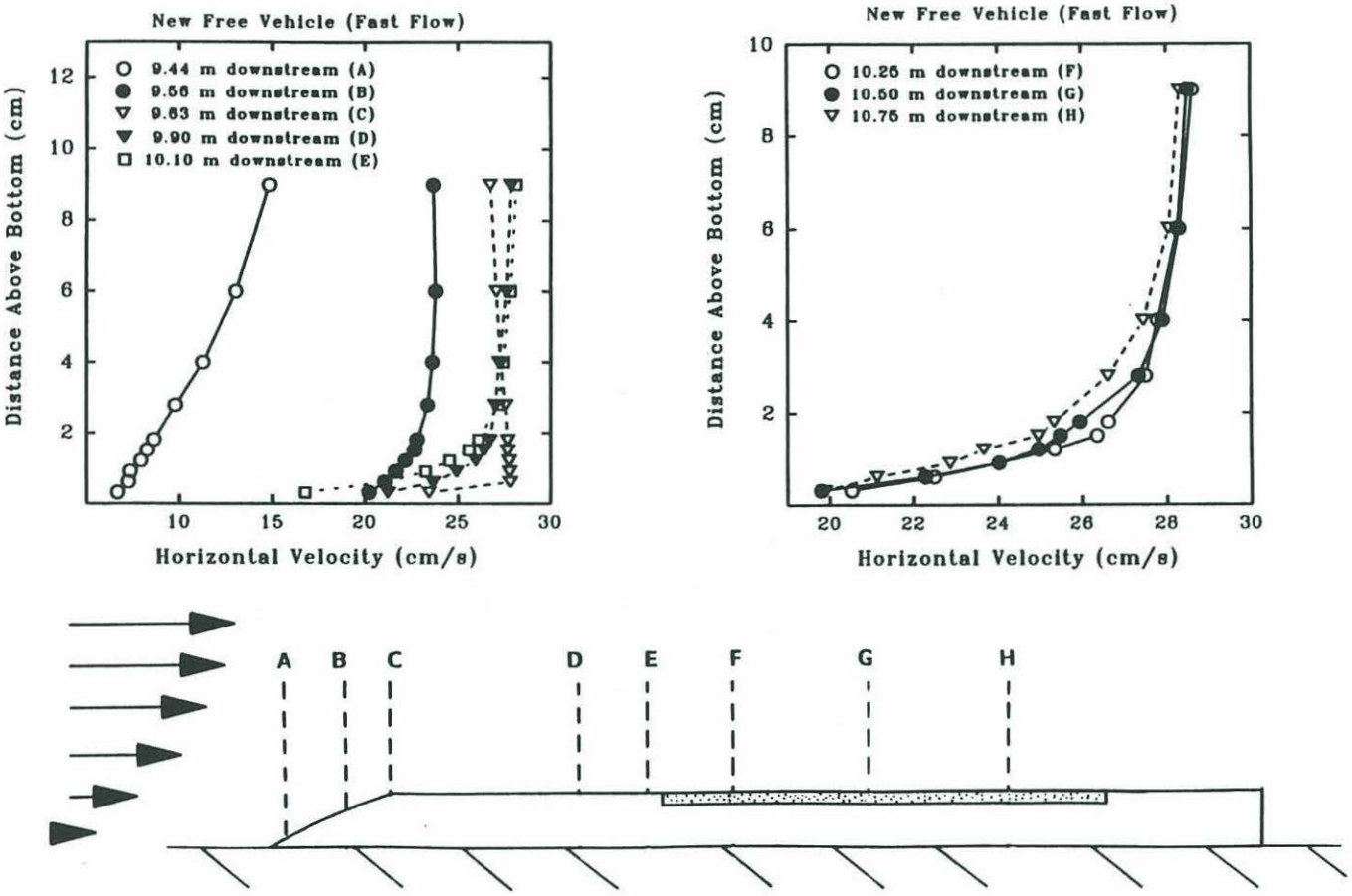


Figure 11. Velocity profiles measured at different points along the New Free Vehicle for fast flow conditions. See caption of Figure 10.

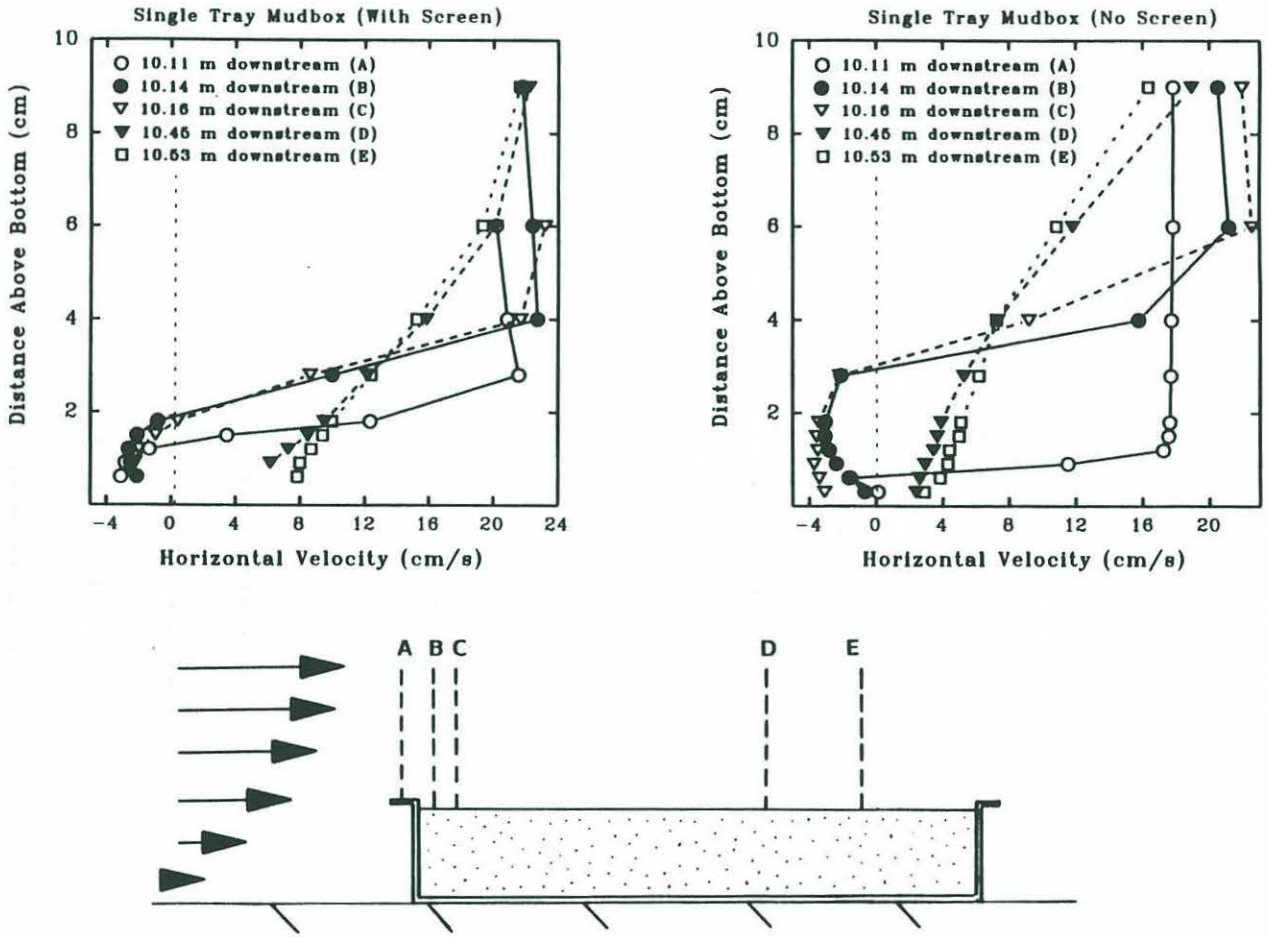


Figure 12. Velocity profiles collected at different points along the Single Tray Mudbox upstream of the sediment surface and over the sediment surface for screened (left) and unscreened (right) trays in slow flow. Points along the mudbox are summarized in the diagram below the plots. Profile points were roughly evenly spaced and based on 6-minute LDV measurements.

boundary layer was slowly developing over the sediment surface, and flow was constantly changing as it progressed downstream. Somewhat surprisingly, the flow over the screened and unscreened mudboxes was very similar. Although screening of this sort is expected to cause increased retention of passive particles (e.g., see Butman, 1989), this effect may be difficult to document with widely spaced profile points.

The Flush Sediment Tray was designed to be placed flush with the ocean bottom, and not surprisingly, the flow over the tray (Fig. 13) was virtually identical to that in the open channel case (Fig. 7). In the profiles measured over the Sediment Tray with the leading edge exposed, modest changes were noted as flow passed over the sediment surface, however, these changes were relatively minor compared with changes observed with any of the other designs. This orientation also represents the worst case scenario; had the exposed lip been on the downstream edge, for example, disturbance would likely have been even less.

## IV. Discussion

Within recent years, the importance of small-scale hydrodynamics has been recognized as an important source of benthic biological heterogeneity (e.g., see reviews by Jumars and Nowell, 1984; Butman, 1987). Despite the fact that many different processes such as nutrient supply, organic flux, sediment deposition and erosion, and larval supply may all be heavily influenced by near-bed hydrodynamics, relatively few studies have employed instrumentation with this issue in mind. Recent studies of larval

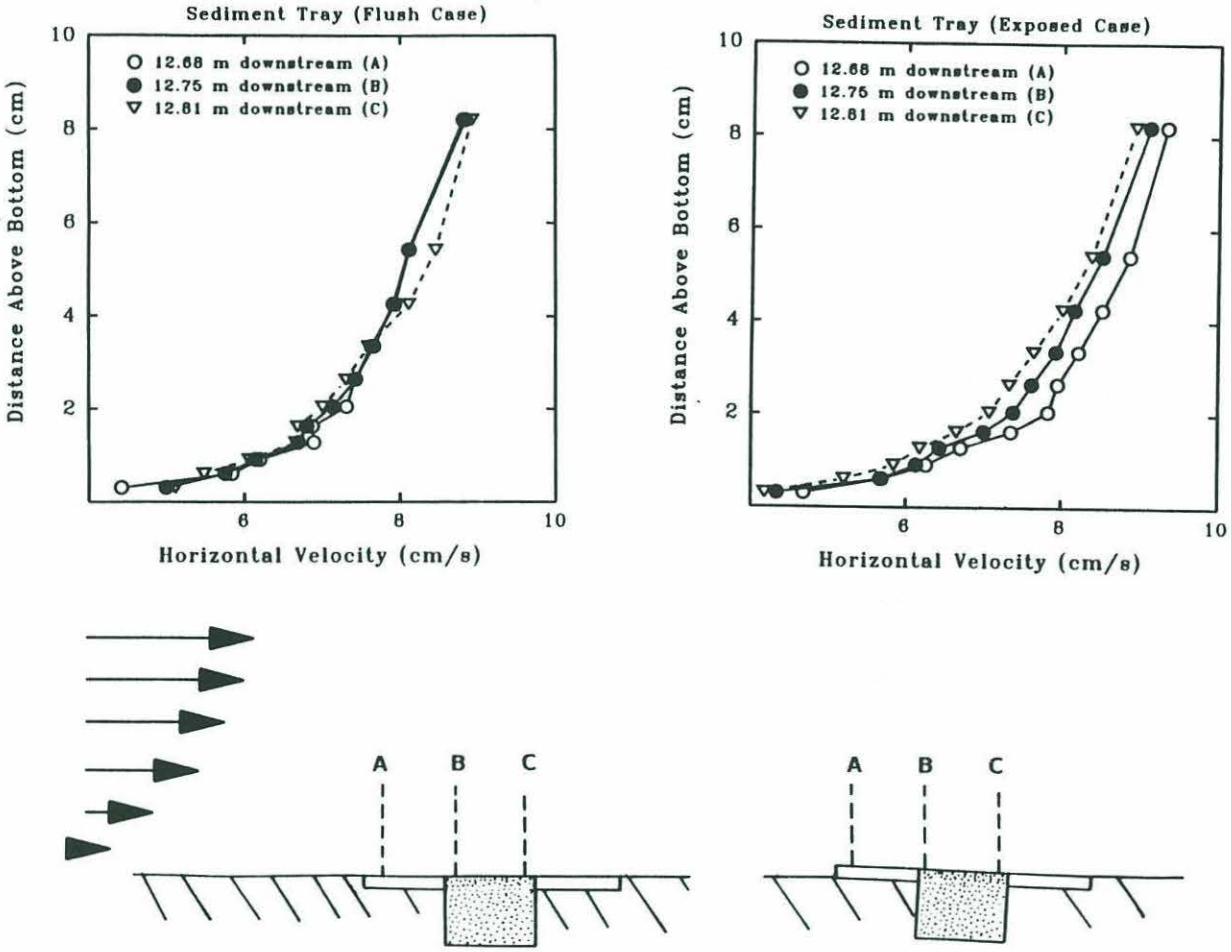


Figure 13. Velocity profiles collected at different points along the Flush Sediment Tray upstream of the sediment surface and over the sediment surface for flush (left) and partially exposed (right) trays in slow flow. Points along the tray are summarized in the diagram below the plots. Profile points were roughly evenly spaced and based on 6-minute LDV measurements.

ecology in natural habitats (e.g., Eckman, 1979, 1983; Butman, 1989) and flume simulations (Pawlik *et al.*, 1991; Butman & Grassle, 1992; Snelgrove *et al.*, 1993) have produced strong evidence that hydrodynamic processes have an important effect on where larvae settle. Thus, there may be good reason to be concerned about the potential hydrodynamic biases that may have been created in studies where sediments were raised above the sea bed both in shallow water (e.g., McCall, 1977; Zajac and Whitlatch, 1982) and in the deep sea (Grassle, 1977; Desbruyères *et al.*, 1980; Levin and Smith, 1984; Desbruyères *et al.*, 1985; Grassle and Morse-Porteous, 1987).

One means of eliminating potential flow artifacts is to place colonization sediments flush with the natural bottom, an approach which has been successfully adopted in several shallow-water studies (Eckman, 1983; Gallagher *et al.*, 1983). Indeed the Flush Sediment Tray shown here has been successfully used in shallow-water (Snelgrove, in prep) and deep-sea (Snelgrove *et al.*, 1992) studies. The flume simulations summarized here (see also Snelgrove *et al.*, 1992) indicate that flow disturbance generated by Flush Sediment Trays is minimal, even when the leading edge is exposed, and that the flow across the tray closely approximates that predicted for the natural environment. Unfortunately, it is not always logistically possible to place trays flush with the ambient sediment, particularly in habitats such as the deep sea that are difficult to access. Thus, it is sometimes unavoidable to have structures protruding above the sediment surface, and efforts must then be directed toward minimizing, rather than eliminating, hydrodynamic disturbance.

Instruments that extend above the ocean bottom and into the benthic boundary

layer create flow disturbance in several different ways, and mudboxes provide an excellent example of the potential flow artifacts that may be created. Because flow must move around a mudbox extending above the bottom, some acceleration must occur. This effect is somewhat minor, however, compared with other potential effects. By raising the mudbox surface into the natural bottom boundary layer, relatively fast flows will move past the mudbox sediment compared with flow over the sediment-water interface (Fig. 1b). The result is that a secondary boundary layer may form on the sediment surface, creating complex, constantly changing flow conditions. Perhaps most important of all, eddies may be shed at various points, potentially creating regions of enhanced shear and local deposition.

These types of flow disturbances were observed in the Old Free Vehicle and Single Tray Mudbox flow simulations (Figs. 8, 9, 12). Qualitatively, flow over these two types of mudbox was quite similar. Because the sediment surface is raised well above the natural seabed, relatively high flow speeds approach the sediment. Over the mudbox sediment and within the natural bottom boundary layer, a thin boundary layer grows over the sediment surface, increasing in thickness as flow moves downstream. Eddies form in front of and behind the sealing gasket of the Old Free Vehicle, and although a gasket is absent from the Single Tray Mudbox, the sediment surface is lower than the rest of the tray and a similar flow effect is produced by the tray itself. Thus, an area of relatively low shear is produced both in front of and behind the gasket, creating depositional areas upstream of the gasket and at the leading edge of the sediment surface. The eddy in front of the gasket may reduce the number of larvae,

adults, sediment grains, or food particles that ever encounter the sediment tray, because this area of very slow flow may cause passively transported material to fall out of suspension. Those particles that make it over the gasket may tend to be entrained in the small eddy behind the gasket. This is further complicated by the fact that the boundary layer over the sediment in this design grows considerably as the flow progresses along the mud. Organisms transported to or settling at two different areas along this axis would encounter completely different flow fields. Furthermore, these measurements were made with flow at right angles to the sediment tray. Flow approaching at an angle, and across the corners of the array, may be even more complex. Clearly, the flow that moves across the Old Free Vehicle and the Single Tray Mudbox is very different from the natural boundary layer flow observed over ocean bottoms.

In designing the New Free Vehicle, many of these potential problems were considered. The sealing gasket was attached to the lid rather than to the sediment trays, eliminating the eddy effect. The sloping edge of the disc surrounding the sediment tray was designed to minimize disturbance to the natural boundary layer, and avoid shedding eddies downstream of the leading edge. Based on the flume simulations shown here, these design goals appear to have minimized hydrodynamic biases. Minimal change was observed in the velocity profiles across the free vehicle sediment, and areas of enhanced deposition and shear (eddies) were not evident. The result was that flow across the sediment tray closely mimicked predictions for natural flow. Because of the compromises necessary to test these vehicles (particularly the bluff-body effect), we do not feel it is appropriate to compute and compare shear velocities over the mudboxes

to those in the open flume bottom. However, the shapes of the boundary layers over the New Free Vehicle and the open flume channel were very similar. Clearly, different designs have very different effects on flow.

Although relatively small, weak eddies may seem unimportant, there is strong evidence that small-scale flow alteration influences settling larvae. Given that typical swim speeds for larvae may be exceeded by mean horizontal flow speeds at distances of only a few millimeters above the bottom (e.g., Butman, 1986a), it is hardly surprising that several field studies have suggested that larvae may be passively entrained in relatively small-scale bottom features such as depressions (e.g., Savidge and Taghon, 1988; Snelgrove, in prep). Although these organisms may be actively responding to organic material that has accumulated in depressions (e.g., VanBlaricom, 1982), there is evidence that passive entrainment may occur for at least some taxa. In flume simulations with competent larvae of *Capitella* sp. I and *Mulinia lateralis*, enhanced settlement was observed in small depressions compared with flush treatments of a similar sediment type (Snelgrove *et al.*, 1993). In fact, *M. lateralis* larvae, in particular, often made a "poor choice" (i.e., settling in depressions containing an unfavorable substrate), probably because of hydrodynamic entrainment. The spatial scale of the eddy created in the small depressions in this experiment with live animals was roughly comparable to the eddies generated in the mudbox simulations described here. Thus, there is very real potential for hydrodynamic modification of larval settlement. Larvae of *Capitella* sp. I and *M. lateralis* are capable of active habitat selection (Butman *et al.*, 1988; Grassle *et al.*, 1992; Butman and Grassle, 1992), yet settlement may be modified

by near-bed hydrodynamics (Snelgrove *et al.*, 1993), suggesting that transport of completely passive particles such as fine-grained sediments and detritus may be modified as they approach structures such as the Old Free Vehicle and Single Tray Mudbox.

There is little doubt that flow disturbances documented here would be somewhat different for different sizes of mudboxes or different flow conditions. Flume simulations with sediment traps, for example, suggest that the trapping characteristics change with flow conditions and trap geometry (Butman, 1986b). Therefore, it is difficult to argue that similar hydrodynamic disturbance in two different habitats is acceptable. Unless flow conditions and flux of passive particles such as fine-grained sediments or detritus are identical between the different habitats, the biases generated by structures, such as the Old Free Vehicle, will probably not be identical.

Although these flume simulations were motivated by an interest in potential hydrodynamic effects on settling larvae, the types of flow disturbance that have been documented here are relevant to many different fields of oceanographic research. The conclusions here are not directed exclusively at larval ecologists, and researchers in other areas of benthic ecology, chemistry, geology, and engineering should exercise similar caution in designing and deploying their sampling gear.

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# Chapter 5

## The role of food patches in maintaining high deep-sea diversity: Field experiments with hydrodynamically unbiased colonization trays

This chapter has been accepted for publication in Limnology and Oceanography with J.F. Grassle and R.F. Petrecca as co-authors. The absence of separately defined "Introduction", "Methods", "Results" and "Discussion" sections reflects the style of the journal.

*Abstract* - To test whether deep-sea macrofaunal diversity is enhanced by specialization on small-scale food patches, we deployed colonization trays by submersible at 900 m depth south of St. Croix for 23 d. Trays were buried flush with the seafloor to minimize potential hydrodynamic bias. Treatments included prefrozen, natural sediment that was unenriched or enriched with either *Thalassiosira* sp. or *Sargassum* sp. Density comparisons and rarefaction analysis indicate that *Thalassiosira* sp. attracted high densities of several taxa of juvenile opportunists, and *Sargassum* sp. trays were colonized by fewer individuals of a more diverse fauna. Ambient faunal diversity was higher and densities lower than enrichment treatments, although unenriched trays did not attain ambient densities. Results suggest that juveniles, rather than adults, specialize on specific patch types, thus contributing to high deep-sea diversity; this bottleneck may be fundamentally different from less diverse, shallow-water macrofaunal assemblages.

Deep-sea, soft-sediment communities are known to be unexpectedly species rich, perhaps rivaling even tropical rain forests in total numbers of species present (Grassle and Maciolek 1992). This richness is surprising given the apparent physical homogeneity of the deep-sea environment compared to other highly diverse habitats such as coral reefs and rain forests. One explanation for this paradox is the patch-mosaic model (Grassle and Sanders 1973), in which small-scale patches of food and disturbance, which are known to occur in the deep sea (Billett et al. 1983; Grassle and Morse-Porteous 1987), create a mosaic on which species may specialize, thus avoiding competition. Since food is almost certainly more limiting in the deep-sea benthos than in most other oceanic soft bottoms, the potential contribution of food patchiness to specialization may be magnified (e.g. Grassle and Morse-Porteous 1987).

One of the better-studied aspects of deep-sea ecology is colonization, for which small-scale experiments have yielded important generalizations on life in deep-sea habitats. For example, colonization is generally thought to be a relatively slow process compared with shallow-water ecosystems (Grassle 1977), except where organic enrichments produce rapid response by opportunistic species (e.g. Desbruyères et al. 1985; Grassle and Morse-Porteous 1987). Unfortunately, logistical constraints have resulted in poorly replicated experiments. Furthermore, past studies have been criticized because colonization trays protruded above the sediment surface creating potential hydrodynamic bias (Smith 1985). Given that hydrodynamics within the benthic boundary layer are now known to be extremely important in determining settlement of some shallow-water larvae (e.g. Butman 1987), it would seem prudent to consider the

possibility that deep-sea larvae are similarly influenced by fine-scale flow processes.

To test the degree of specialization on patches of organic matter by deep-sea macrofauna, we deployed a series of colonization trays containing ambient sediment without and with added organic matter. Trays were enriched with either *Sargassum* sp., a seaweed that has been observed in the deep sea (Grassle and Morse-Porteous 1987), or *Thalassiosira* sp., a cosmopolitan diatom genus chosen to mimic seasonally deposited phytodetritus on the deep-sea floor (Billett et al. 1983). Trays were deployed for 23 d at 900 m depth near St. Croix, U.S. Virgin Islands. To avoid potential hydrodynamic bias, colonization trays were designed specifically so that a submersible could bury them with the experimental sediment surface flush with the ocean floor.

Each sediment tray (Fig. 1) consisted of a large circular Delrin plastic disk (40-cm diameter, 2-cm thick) and a nylon cup (11.3-cm diameter, 10-cm depth, and 1.3-cm thickness). A nylon mesh bag (20-μm openings) was fitted inside the cup and bolted in place at its open end between the cup and the disk. Bags were filled with sediment so that the sediment surface was smooth and flush with the disk. Large holes, drilled in the side of the cup, allowed pore-water exchange through the mesh. The bottom of the cup consisted of a nylon ring (11.3-cm diameter) used to bolt 300-μm reinforcing mesh to the bottom of the cup, providing support for the sediment-filled bag and allowing access through the bottom for sediment extrusion.

Nylon posts at the periphery of the tray were used to position and secure the lid. The larger, solid posts (E) helped guide the recovery lid (G) into place. The lid was pushed down from above, bending the smaller, flexible locking posts (F) until they

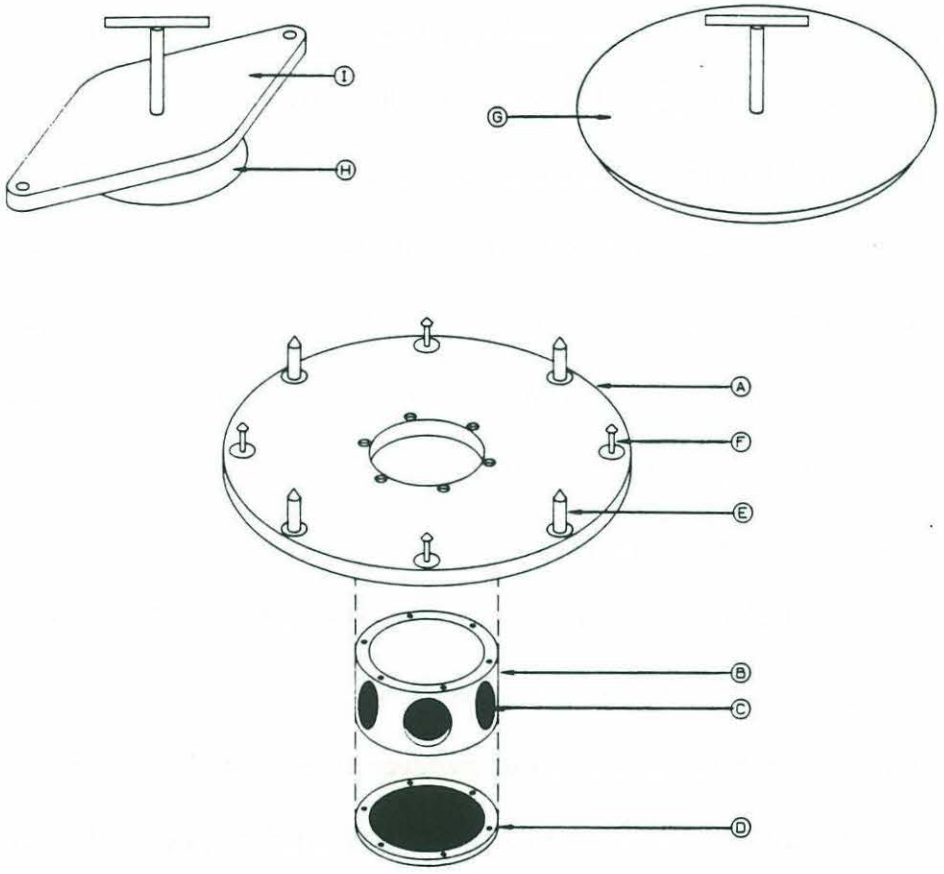


Fig. 1. Side view of sediment tray used in colonization experiments showing Delrin disk (A), cup (B), mesh bag (C), removable screen bottom (D), guideposts (E), locking pins (F), recovery lid (G), rubber gasket (H), and deployment lid (I). Depth of cup is 10 cm and diameter of disk is 40 cm.

locked the lid in place. A neoprene rubber gasket ring, contained within a circular groove cut on a 45° angle to the surface of the lid, proved effective in preventing sediment leakage during recovery or deployment of trays. A smaller, elliptical deployment lid (H) with a similar sealing gasket (I) was used for deployment; cotter pins attached to polypropylene line locked the lid in place.

The tray design represents a compromise between hydrodynamic considerations and practical constraints. For example, the guide posts and flexible pins were required to attach a sealing lid during deployment and recovery, but they unfortunately also disturb the flow over the tray. To reduce this effect, the posts were located 10 post diameters from the edge of the cup. This positioning assured substantial dissipation of the flow disturbance before the fluid reached the sediment in the cup. The size of the tray was constrained by the desire to place the tray flush with the ocean bottom; the larger the tray the more difficult such placement.

Important aspects of the boundary-layer flow over the surface of sediment contained in the tray were measured in a laboratory flume to evaluate the effectiveness of this tray design in avoiding flow disturbance under realistic deployment and flow conditions. Flow simulations were conducted in the 17-m flume at the Coastal Research Laboratory at Woods Hole Oceanographic Institution. Velocity profiles over the tray were measured using a laser-Doppler velocimeter (LDV) in a flow typical of many deep-sea environments (shear velocity, $u_*$, was approximately 0.50 cm $s^{-1}$, estimated using the Karman-Prandtl log-profile relationship). The sediment tray was placed inside a 48-by-48 cm, sediment-filled, removable box located 12 m from the entrance of the

flume. Boundary-layer flow in this test area was fully developed. One series of LDV profiles was taken with the tray flush with the flume bottom (Fig. 2A) and another series with the upstream edge of the tray purposely exposed (Fig. 2B). These tray orientations corresponded to best- and worst-case scenarios based on our own experience with deep-sea deployments near St. Croix. Shear velocities were calculated from velocity profiles assuming an equilibrium boundary layer, as by Gross and Nowell (1983), using 8 points within an estimated logarithmic (log) layer between 1.27 and 8.2 cm above the sediment surface. The logarithmic layer, which is a portion of the boundary layer where velocity varies logarithmically with height above bottom, is often used to characterize flow.

The flume simulations of tray deployments showed that profiles upstream of the tray were nearly identical to profiles at various points in front of and across the contained sediment when the tray was flush with the surrounding seafloor (Fig. 2A). Neither the shapes of the profiles nor the shear velocities changed appreciably across the tray. For the tray with the leading edge exposed (Fig. 2B), flow deceleration was evident upstream of the sediment container, which was partly an artifact of containing the tray in the flume channel. In the field, the flow would be free to move around, as well as over, the tray, and the upstream flow acceleration would be reduced. Thus, these profiles may exaggerate the flow disruption that this tray orientation may cause. Nonetheless, velocity profiles over the protruding tray remained relatively constant and the boundary layer completely recovered by the time it reached the downstream area of the contained sediment (profiles 3 and 4 in Fig. 2B). It is not yet possible to evaluate whether the minor upstream disruption associated with the exposed tray could influence

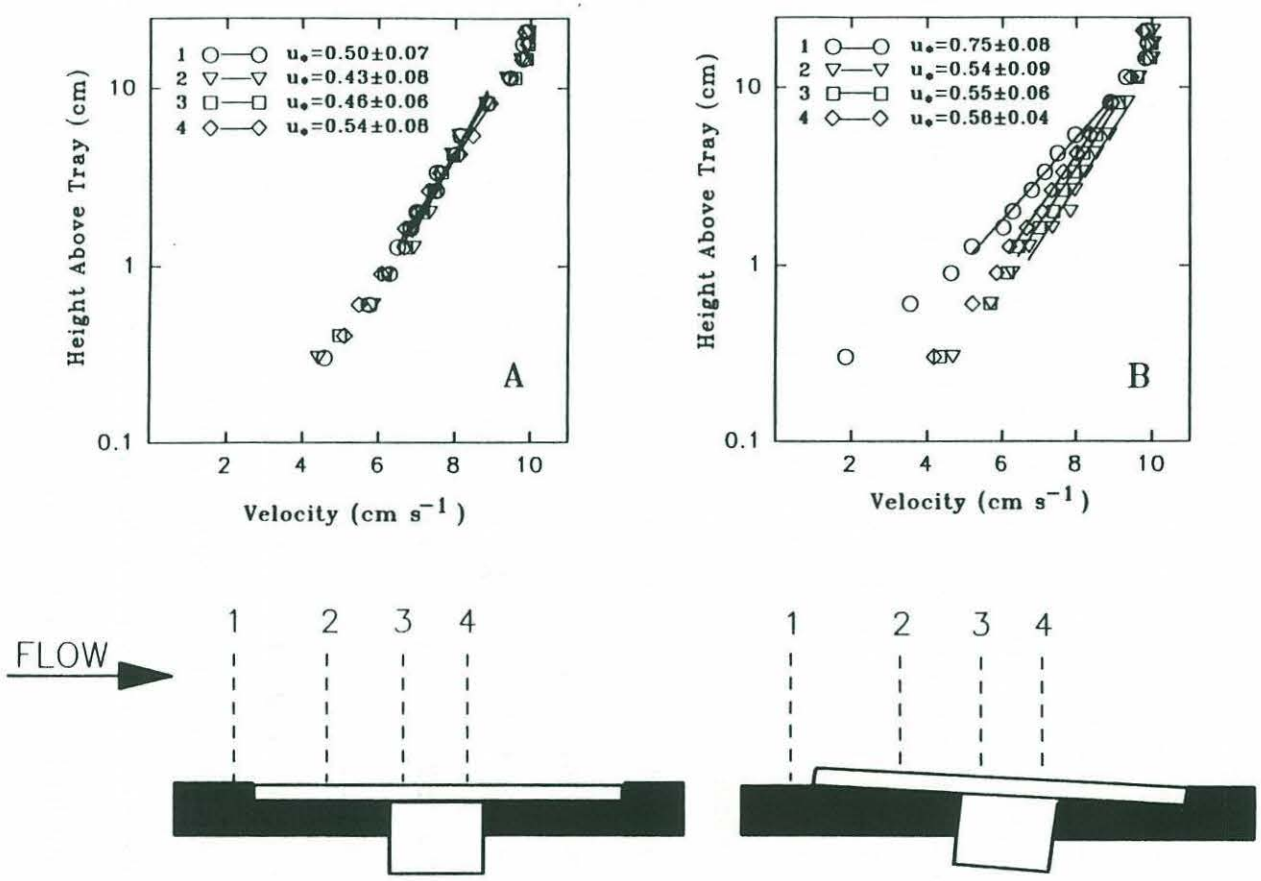


Fig. 2. A. Diagrammatic representation of laser-Doppler velocimeter (LDV) profiles at selected positions with the tray surface flush with the flume floor: (1) 2 cm in front of leading edge of tray, (2) 8 cm behind leading edge of tray, (3) 15 cm behind leading edge of tray, over upstream half of sediment, (4) 21 cm behind leading edge of tray, over downstream half of sediment. Shear velocity ($u_*$) was determined from the Karman-Prandtl log-profile relationship: $U(z) = u_* / \kappa \ln ( z / z_o )$, where $\kappa$ = von Karman's constant (0.41); U (z) = mean velocity at height z above bottom; $z_o$ = roughness parameter. 95% confidence intervals are given for each of the $u_*$ estimates. B. As in panel A except leading edge of tray is fully exposed (approximately 2 cm above sediment surface).

the colonization pattern. Compared to other tray designs, however, this flow disturbance is modest (Snelgrove et al. in prep).

Colonization experiments were conducted at 900-m depth on a relatively flat area 14.4 km southwest of St. Croix (17°35.38'N, 64°47.52'W) in May and June 1989. A large volume of the carbonate sediment characteristic of the area was collected during the first in a series of submersible dives at the site. Sediment was frozen and then thawed to fill the sediment trays prior to deployment. Three treatments were replicated five times; no enrichment, 1.2% enrichment by dry weight of organic carbon with ground brown algae (*Sargassum* sp.), and 1.0% enrichment with diatom paste (*Thalassiosira* sp.). Enrichments were selected to be higher than in ambient sediment, which contained ≈ 0.7% carbon. Concentrated paste (Coast Oyster Company, Seattle; purchased with no preservative) was used in the case of *Thalassiosira* sp. because it was logistically the only way to create the level of organic enrichment we desired. *Sargassum* sp. was collected by small boat off the coast of Florida and frozen for several months before the experiment. To avoid the hydrodynamic complication of algae protruding above the sediment surface, the *Sargassum* sp. was ground into small particles with a food processor. Organic material was mixed homogeneously into the top 2 cm of sediment.

The submersible carried three trays to the bottom per dive, including one of each of the three treatments, and excavated depressions in the bottom sediment of approximately the same depth and shape as the sediment containers. By moving each tray around slightly and applying pressure, trays were positioned to be relatively flush

with surrounding sediment. The variable hardness of the bottom resulted in trays sometimes protruding slightly (see Fig. 2). Because of the deployment sequence, however, this bias was haphazardly interspersed among treatments. Trays were deployed and recovered in the same sequence so that all trays remained in situ for 23 d. The upper 2 cm of recovered samples, where enrichment material occurred, were sieved aboard ship over nested 300- and 63-µm sieves, and then preserved in buffered 4% formaldehyde. Samples were later transferred to 80% ethanol, stained with Rose Bengal, and sorted under a dissecting microscope. Organisms were identified to the lowest possible taxonomic level, which was often limited by the absence of mature specimens. ALVIN-style box corers (e.g. Grassle and Morse-Porteous 1987), which enclose an area of 225 $cm^2$ and penetrate to approximately 10 cm, were used to obtain faunal samples from the ambient sediment. These samples were processed in a manner similar to the trays. For comparison, individuals from only the upper 2 cm were sieved on nested 300- and 63-µm sieves. Relatively few individuals (< 5%) were found in the 63-µm fraction, but macrofaunal taxa from this fraction were included in our totals for completeness. Meiofaunal taxa, which were numerically rare, were not enumerated.

Species-by-species comparisons among treatments is extremely tenuous due to the need to adjust type I error to compensate for multiple independent comparisons. This problem is compounded in deep-sea communities because of the many rare species (e.g. Grassle and Morse-Porteous 1987). We have therefore chosen to do between-treatment individual species comparisons for only the five most abundant species and use community parameters to compare the complete faunas including all species.

Hurlbert rarefaction was chosen for community contrasts since it is the least problematic of the "diversity" measures and is sensitive to rare species (Smith and Grassle 1977). Confidence intervals for pooled samples were calculated with the Smith and Grassle (1977) variance estimator.

Total numbers of macrofauna in the enrichment treatments greatly exceeded numbers in the adjacent sediment, while unenriched trays (controls) did not attain ambient densities (Fig. 3). *Thalassiosira* sp. attracted the highest densities of the most abundant colonizers, though *Sargassum* sp. also attracted large numbers. Hurlbert rarefaction analysis indicated that many individuals of few species colonized *Thalassiosira* sp. treatments and fewer individuals of more species colonized *Sargassum* sp. trays (Fig. 4A). While the rarefaction curve for *Thalassiosira* sp. fauna was asymptotic when all individuals were included, the curve for *Sargassum* sp. was not. Despite low densities, diversity in unenriched trays was more comparable to ambient sediments (Fig. 4B) than to enrichment trays. Those species that dominated *Thalassiosira* sp. enrichment trays were common, though less abundant, in *Sargassum* sp. treatments (Fig. 3). Species that dominated enrichment treatments were also relatively rare in unenriched sediment trays.

The fauna colonizing sediment trays was markedly different from that found in ambient sediment. The most common colonizers were juvenile polychaetes and crustaceans, which were rare or absent from ambient samples. In fact, all species colonizing trays were much lower in density in ambient sediment, and few of the species observed in ambient sediment colonized the trays.

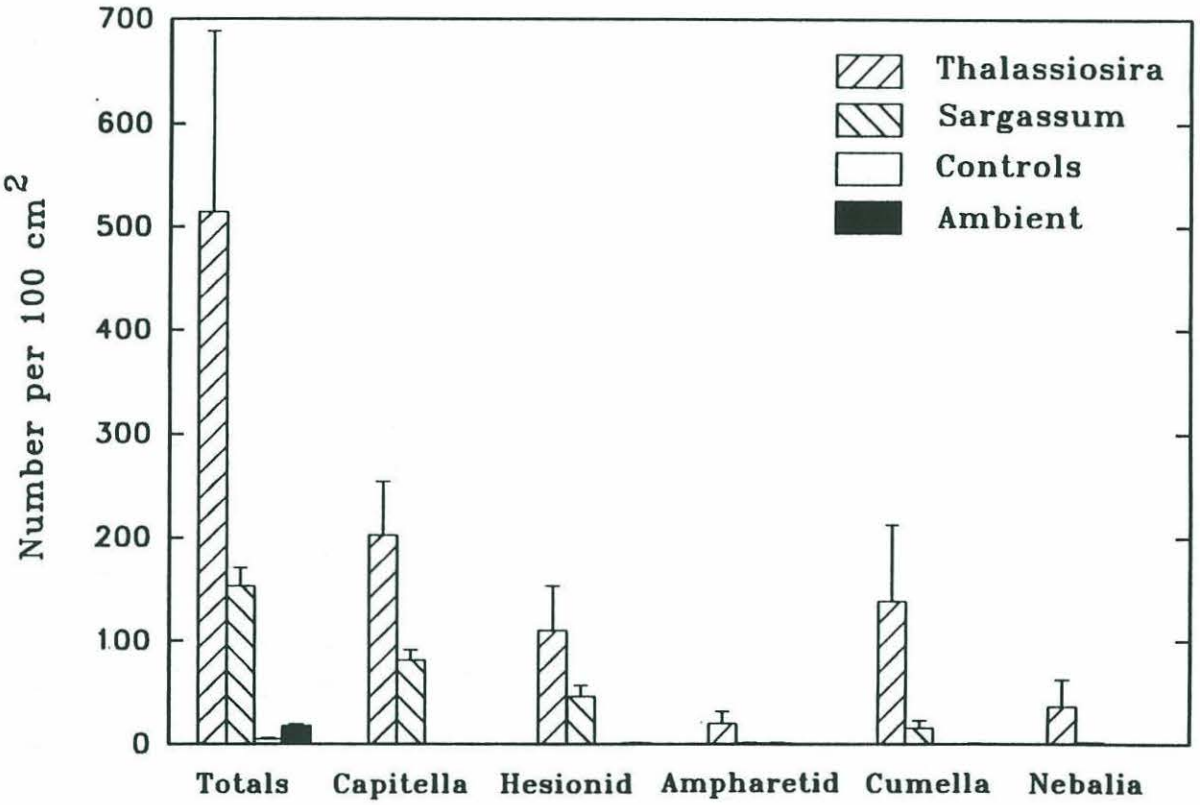


Fig. 3. Bar graph showing mean densities and one standard error for the most common species colonizing each of the three treatments (n = 5) relative to ambient densities (n = 4). Individuals from the upper 2 cm of sediment in the trays or cores are included. Though most organisms were retained on a 300-µm sieve, we have included macrofaunal organisms retained on a 63-µm screen as well.

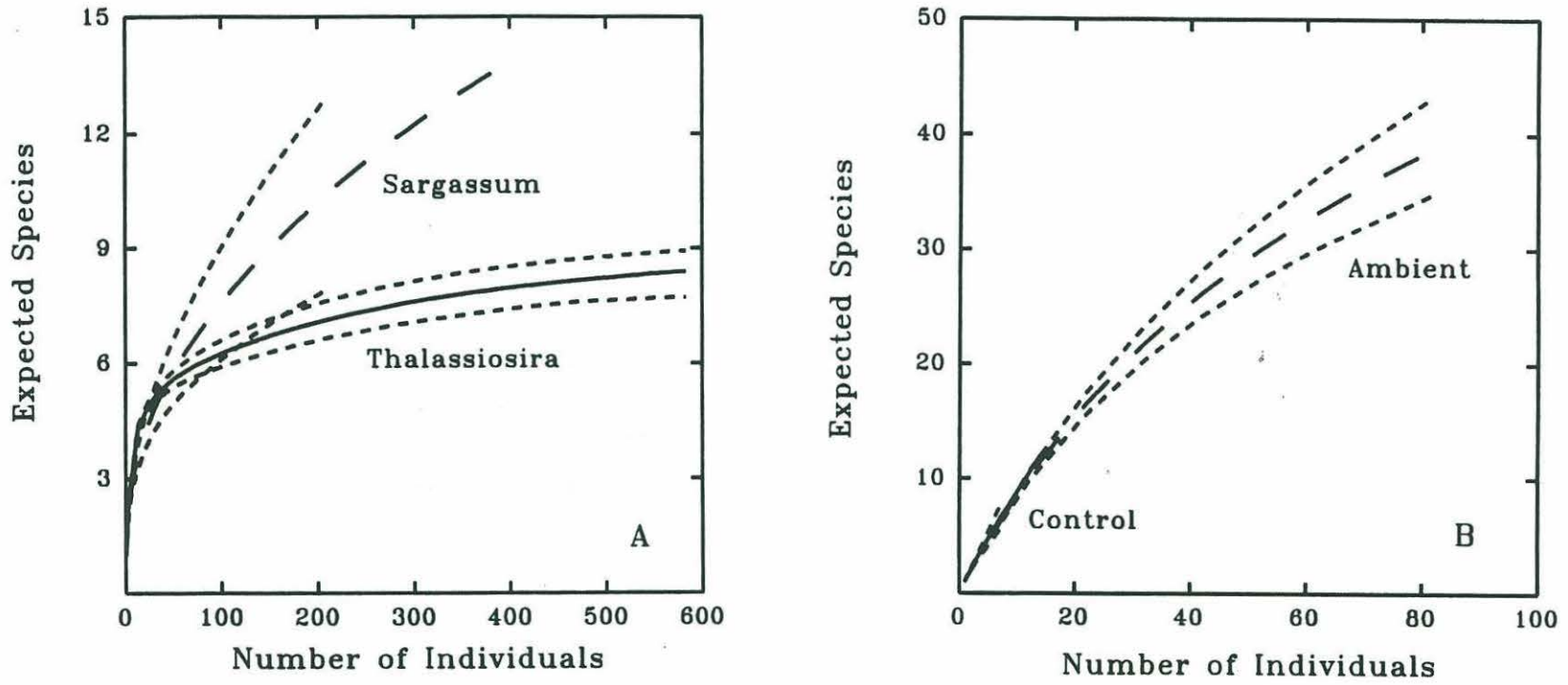


Fig. 4. A. Number of Individuals plotted against Expected Species (Hurlbert rarefaction) based on random combinations of the five replicates. Solid line represents *Thalassiosira* sp.- enriched trays, dashed line denotes *Sargassum* sp.-enriched trays. Dotted lines denote 95% confidence intervals. B. As in panel A, except dashed line denotes ambient fauna (n = 4), and solid line denotes control trays (n = 5). A different scale was necessary relative to panel A to distinguish plot lines from the Y axis.

Our deep-sea experiments provide the first hydrodynamically unbiased data on deep-sea colonization using sediment trays. The large numbers of juveniles in our trays underscores the need to consider fine-scale flow effects since some settling planktonic larvae (and perhaps juveniles) are very sensitive to flow (Butman 1987), at least in comparison with stronger swimming adults. This design is an improvement over sediment trays that sit elevated on the order of 10 cm above the seafloor (e.g. Grassle 1977; Desbruyères et al. 1985; Grassle and Morse-Porteous 1987). Flume simulations of these elevated trays indicated dramatic, tray-induced flow disturbances that resulted in substantial differences between the flow regime over the experimental sediment surface and the natural seafloor, including large eddies, flow acceleration, and variable embedded boundary-layer thickness (Snelgrove et al. in prep). Flume simulations of our tray design indicated that the flow that settlers encountered was similar to the flow over the adjacent bottom, and even poorly deployed trays had flow characteristics approximating those over the ambient sediment.

The elevated densities and treatment-specific responses indicate active selection for organic matter by at least some infaunal species. Aspects of *Sargassum* sp. that may make it more complex organically include susceptibility to decomposition, presence of antiherbivory compounds, and lower nitrogen content. Whether these factors made it less attractive to more opportunistic species or more attractive to some rarer species is unclear. Other potential contributing factors include particle size, microbial content, pore-water oxygen content, and nutritional value. Whatever the cause, it appears that the enriched trays attracted somewhat different faunas, with fewer individuals of more

species colonizing *Sargassum* sp. and many individuals of relatively fewer species colonizing *Thalassiosira* sp. The fauna colonizing unenriched trays, which differed from enriched trays, may have responded to the modest enrichment resulting from organisms present in the sediment at the time it was frozen or to the absence of potential competitors or predators. The slow response to unenriched trays suggests that food, rather than space, is limiting in this environment.

The preponderance of juveniles in enriched trays suggests that elevated organic matter may act as a competitive release for colonizing juveniles, allowing relatively uncommon species to flourish. Thus, a deep-sea competitive bottleneck (Jumars et al. 1990) may prevent these juveniles and larvae from coexisting with other species under conditions where food is more limited in amount and content (e.g. unenriched trays, ambient sediment): however, patches of specific food resources prevent them from going extinct. Such bottlenecks might allow species to colonize only under very specific conditions, thus mitigating competition and supporting diversity. The low numbers of colonizing adults, however, may be a product of the tray design, which precludes colonization by lateral movement from surrounding sediments. Trays isolated from the surrounding sediment showed lower colonization rates than similar azoic sediment where within-sediment migration is possible (Smith et al. 1986). Nonetheless, the rapid response to enrichment and high densities of colonizers compared to ambient sediments in our study indicate that within-sediment migrators would have to be very fast invaders and either very strong competitors or voracious predators to significantly alter the patterns observed.

Colonization of control trays, though modest, represents one of the fastest rates for unenriched sediment in the deep sea to date, even though densities in adjacent sediments are relatively low (for summary see Grassle and Morse-Porteous 1987). This is also true for enrichment trays, where response was far more rapid than that observed in any previous enrichment study. Because there are so few colonization studies of this nature in the deep sea and experiments have been conducted under very different conditions, it is difficult to determine why densities in our study are so high. Though our smallest sieve size was smaller than in previous studies, the vast majority of the organisms we collected were retained on a 300-μm screen, similar, for example to the sieve size used by Grassle and Morse-Porteous (1987) where densities were much lower, so this difference cannot explain our result. The two most unusual features of our study, however, are the short duration of experiments (23 d) and the placement of trays flush with the ocean bottom. The importance of these variables should be established in future experiments.

Ultimately, the deep-sea paradigms that have arisen from colonization tray studies appear to hold up in our hydrodynamically unbiased colonization estimates. Deep-sea colonization is indeed slower than in shallow water (Grassle 1977). Although results from the present study indicate that the proportion of background densities attained in unenriched sediment in this study is higher than previously estimated for the deep sea, the rate of colonization was still considerably slower than in shallow-water studies conducted over a similar interval. For example, Gallagher et al. (1983) used flush, hydrodynamically unbiased trays to evaluate shallow-water colonization and found

that even without enrichment, colonization densities actually exceeded ambient densities.

A contemporaneous disequilibrium model for maintenance of high-diversity, deep-sea communities requires that patches of food and disturbance exist in the deep sea, and that species differentially respond to alternative patch types (Grassle and Sanders 1973). Feeding disturbances and patches of organic matter are known to occur (Billett et al. 1983; Grassle and Morse-Porteous 1987), and response by deep-sea species has been documented for macrofauna (e.g. Grassle and Morse-Porteous 1987). Little evidence is available concerning patch partitioning, however, and our data provide initial evidence for a somewhat specialized biological response. Topographic variation created by biological activity (e.g. Smith et al. 1986) may add further heterogeneity. These structures may persist in the deep sea longer than they persist in shallow water, favoring longer-term deposition of specific food types, colonization of somewhat specialized species or both (Aller and Aller 1986). Organic composition, age and bacterial content may be compounded with differences in microtopography and initial colonizers to further enhance the mosaic. All of these sources of persistent microheterogeneity may potentially contribute to the high diversity of deep-sea infauna but remain less important in shallow water where they are likely to be more transient. This transience may be the fundamental difference between high diversity deep-sea habitats and their low diversity, shallow-water counterparts.

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# CHAPTER 6

## Macrofaunal Response to Artificial Enrichments and Depressions in a Deep-Sea Habitat

## ABSTRACT

To test whether small-scale patches of food and disturbance contribute to the unexpectedly high macrofaunal diversity of the deep sea, and evaluate the relative importance of active habitat selection for different patches of food and disturbance versus passive deposition of colonizing fauna, sediment tray and artificial depression colonization experiments were conducted on the deep-sea floor at 900-m depth, south of St. Croix, U.S. Virgin Islands. Trays and depressions were unenriched (Unenriched Controls) or enriched with either *Thalassiosira* sp. or *Sargassum* sp. Concurrent deployment of different types of enrichment and disturbance made it possible to evaluate whether macrofauna specialize on these patches. Depressions create a hydrodynamic regime that traps passive particles, allowing tests of the relative importance of active selection of different patch types versus passive deposition for abundant colonizers. By specializing on different patch types, organisms may avoid species interactions that might lead to competitive exclusion, thus contributing to deep-sea diversity. After 23 d, total densities and densities of the four abundant colonizers (*Capitella* spp., *Nereimyra* sp., *Cumella* sp. and *Nebalia* sp.) were extremely high in enriched trays, despite relatively low ambient densities. Densities in Unenriched Control Trays were very low, and did not attain ambient densities. After 24 d, total densities in all depression treatments were considerably lower than in enriched tray treatments, and only *Sargassum* Depression densities exceeded those in the ambient environment. Lower densities of organisms in depression treatments compared with trays, and the different densities observed in different depression treatments suggest that the dominant colonizers were

highly active and selective and were not passively entrained in depressions. Analysis of samples indicated that trays and depressions were very different, and *Sargassum* Depressions were very different from other depression types. A strong difference was not observed between fauna in ambient sediments and *Thalassiosira* sp. or Unenriched Control Depressions, perhaps because *Thalassiosira* was dropped in depressions on the sediment surface and may have been more readily available to consumers and more rapidly consumed than in trays. Hurlbert rarefaction indicated that *Thalassiosira* Trays were colonized by a lower diversity fauna than *Sargassum* Trays, and Unenriched Control Trays were colonized by very low densities of a fauna that was comparable in diversity to the ambient community. Diversity in *Sargassum* Depressions was higher than in enriched trays but lower than in other artificial depressions and the ambient fauna. *Thalassiosira* Depressions and Unenriched Control Depressions were comparable in diversity to ambient fauna and natural depressions, which were highly diverse. These experiments suggest that fauna may respond quickly and selectively to artificial food patches and disturbance, and this fauna is different from that observed in the ambient sediment. Thus, a patch mosaic may be part of the reason for the species richness of the deep sea. The different, highly diverse, fauna observed in natural depressions compared with flat ambient sediment suggests that natural analogs of these experiments may indeed contribute to high deep-sea diversity.

*1. Introduction*

The recent suggestion that deep-sea ecosystems may actually rival tropical rain forests in species richness (Grassle and Maciolek, 1992) makes the study of immense diversity in a relatively homogeneous habitat such as the deep sea all the more intriguing. One explanation for this paradox is the patch-mosaic model, in which small-scale patches provide organic and spatial microhabitats for infaunal organisms, thus diminishing species interactions (Grassle and Sanders, 1973). The applicability of the patch-mosaic model has gained indirect support from the growing body of literature on patchiness in the deep sea. One type of patch is created by carbon flux to the sea floor, and this flux may exhibit dramatic temporal (Deuser and Ross, 1980; Honjo, 1982; Billett *et al.*, 1983) and spatial (Grassle and Morse-Porteous, 1987; Suchanek *et al.*, 1985) variation. Carbon sources may range from phytodetritus (Billet *et al.*, 1983) to macroalgae (Grassle and Morse-Porteous, 1987) to carrion parcels (Stockton and DeLaca, 1982; Smith *et al.*, 1989). Other forms of disturbance can create patches; biological activity may rapidly alter the surface topography of deep-sea sediments through movement of animals within and across the sediment (Wheatcroft *et al.*, 1990), or through the feeding activity of motile predators (Smith, 1986). Clearly, the deep sea is not as stable and homogeneous as was once thought (e.g, Sanders, 1968).

A variety of taxa respond to carbon flux and disturbance in the deep sea (reviewed by Gooday and Turley, 1990). Megafaunal densities may rapidly increase in response to sedimented phytodetritus (Billett *et al.*, 1983) and fish carcasses (e.g., Dayton and Hessler, 1972). Some species of benthic foraminifera also occur in high

densities in the presence of phytodetritus (Gooday, 1988) and artificial and natural disturbance (Levin *et al.*, 1991). Macroalgae (Grassle and Morse-Porteous, 1987; Grassle *et al.*, 1988) and disturbance generated by feeding-mound formation (Kukert and Smith, 1992) have both been shown to result in changes in relative abundance of dominant species. Communities may change not only in response to carbon input but also to other forms of disturbance. Biological disturbance as varied as megafaunal feeding (Smith, 1986) to polychaete feeding (Thistle, 1979) may also influence community composition, and biologically produced structures such as feeding mounds (Levin *et al.*, 1991; Kukert and Smith, 1992), mud tests (Thistle and Eckman, 1990) and Xenophyophorea (Levin *et al.*, 1986) also have associated faunas that differ from that in the ambient environment. Depressions formed by burrowing (e.g., Aller and Aller, 1986), infaunal sediment reworking (e.g., Nowell *et al.*, 1984) and feeding activity of mobile macrofauna may also contribute to patchiness, however, the impact of these activities on biodiversity is not known.

In all of the studies that have been conducted on the effects of patches on infaunal biodiversity, a different suite of species tended to dominate disturbances or organic patches relative to the ambient fauna, however, most of these studies were conducted in very different areas and focussed on a single patch type. Thus, it is unclear whether different forms of disturbance or patch type result in different faunal response within a habitat. With the exception of comparisons of enriched and unenriched sediments (Grassle and Morse-Porteous, 1987; Desbruyères *et al.*, 1985), no study has demonstrated different biological responses to different types of disturbance

or patch within a given area of the deep sea. Although a single type of disturbance response within a community may enhance diversity, different responses to different disturbances in time and space are necessary if the immense faunal diversity of the deep sea is the direct result of a patch mosaic.

We have reported elsewhere on experiments designed to determine whether different species respond to different "patch" types (Snelgrove *et al.*, 1992). Replicated colonization trays that were unenriched or enriched with either *Sargassum* sp. or *Thalassiosira* sp. were deployed flush with the seafloor by submersible at a site south of St. Croix, U.S. Virgin Islands. Large numbers of a low-diversity fauna colonized *Thalassiosira* Trays, lower numbers of a higher diversity fauna colonized *Sargassum* Trays, and very lower densities of a very diverse fauna colonized Unenriched Trays. Relative species composition of colonizers of trays was markedly different from that in the ambient sediment. Thus, different species responded to different patch types, a finding which supports the patch-mosaic model. We expand on those findings here and compare results to a second type of experiment where artificial depressions were enriched in a similar manner. Artificial depressions are a more realistic analog to natural deep-sea processes than colonization trays, and thus allow a more comprehensive interpretation of colonization processes.

Because of the hydrodynamic regime associated with depressions (see reviews in Nowell and Jumars, 1984; Snelgrove *et al.*, in press), passive particles that range in size from phytodetritus (e.g., Thiel *et al.*, 1988) to macroalgae (Grassle and Morse-Porteous, 1987) tend to accumulate; thus natural depressions are a mechanism by which

organic patches may form in deep-sea (and other) habitats. As an experimental manipulation, artificial depressions have another advantage over trays. In the present study, trays were deployed flush with the sea floor to reduce the potential hydrodynamic bias that has generated criticism (Smith, 1985) of a number of previous deep-sea colonization studies (Grassle, 1977; Levin and Smith, 1984; Desbruyères *et al.*, 1985; Grassle and Morse-Porteous, 1987). Nonetheless, trays isolated the contained sediment from the surrounding sediment, preventing burrowing fauna from invading through the sediment (Kukert and Smith, 1992). Indeed, organisms may be less likely to colonize elevated trays than artificial sediment mounds (Smith *et al.*, 1986), suggesting that burrowing may be an important colonization mode into small-scale patches. Thus, by allowing invasion of burrowing fauna through the sediment, artificial depressions offer a more realistic analog to natural small-scale disturbances and patches.

The passive trapping characteristics of depressions also allow us to address another important issue. Mounting evidence suggests that colonization in shallow-water, soft-sediment ecosystems may be heavily constrained by near-bed hydrodynamics (reviewed by C.A. Butman, 1987). In a shallow sandflat, elevated densities of colonizers have been observed in artificial depressions *in situ* compared with comparable flush treatments (Savidge and Taghon, 1988), although it is unclear whether this was an active response by larvae to organic matter accumulating in depressions or passive larval entrainment. Flume studies of larval settlement in depressions without the potentially confounding effects of suspended sediment and organic matter suggest that larval encounter with the substratum in depressions may be passively enhanced by the trapping

flow characteristics, but escape from depressions may occur if the substratum is unsuitable for settlement (Snelgrove *et al.*, in press). Artificial depressions on the deep-sea floor allow us to test whether colonization is an active process or whether settling colonizers are distributed onto the bottom like passive particles. Because different macrofaunal responses were observed to different organic treatments in flush trays (Snelgrove *et al.*, 1992), colonization by dominant species was active, however, larvae may still be influenced by near-bed hydrodynamics. Thus, if larvae are dependent on near-bed transport, comparable settlement ("trapping") might be expected in different depression types. Highly active colonization should result in colonization patterns that differ between depression treatments and are comparable to corresponding tray treatments.

Thus we are presenting data to test whether different fauna respond to artificial patches of food and disturbance, and to what degree response is active versus passive. Faunal data from experiments are also compared to the ambient community, including samples taken from natural depressions, to evaluate whether colonizing fauna are a specialized subset of the ambient fauna and whether natural depressions are a natural analog to the experimental manipulations.

## 2. Materials and Methods

*a. Experimental site.* Experiments were conducted in late May through June 1989, south of St. Croix, U.S. Virgin Islands (Fig. 1), using the Johnson-SeaLink submersible. The bottom station was located at 900 m in a relatively flat area conducive to

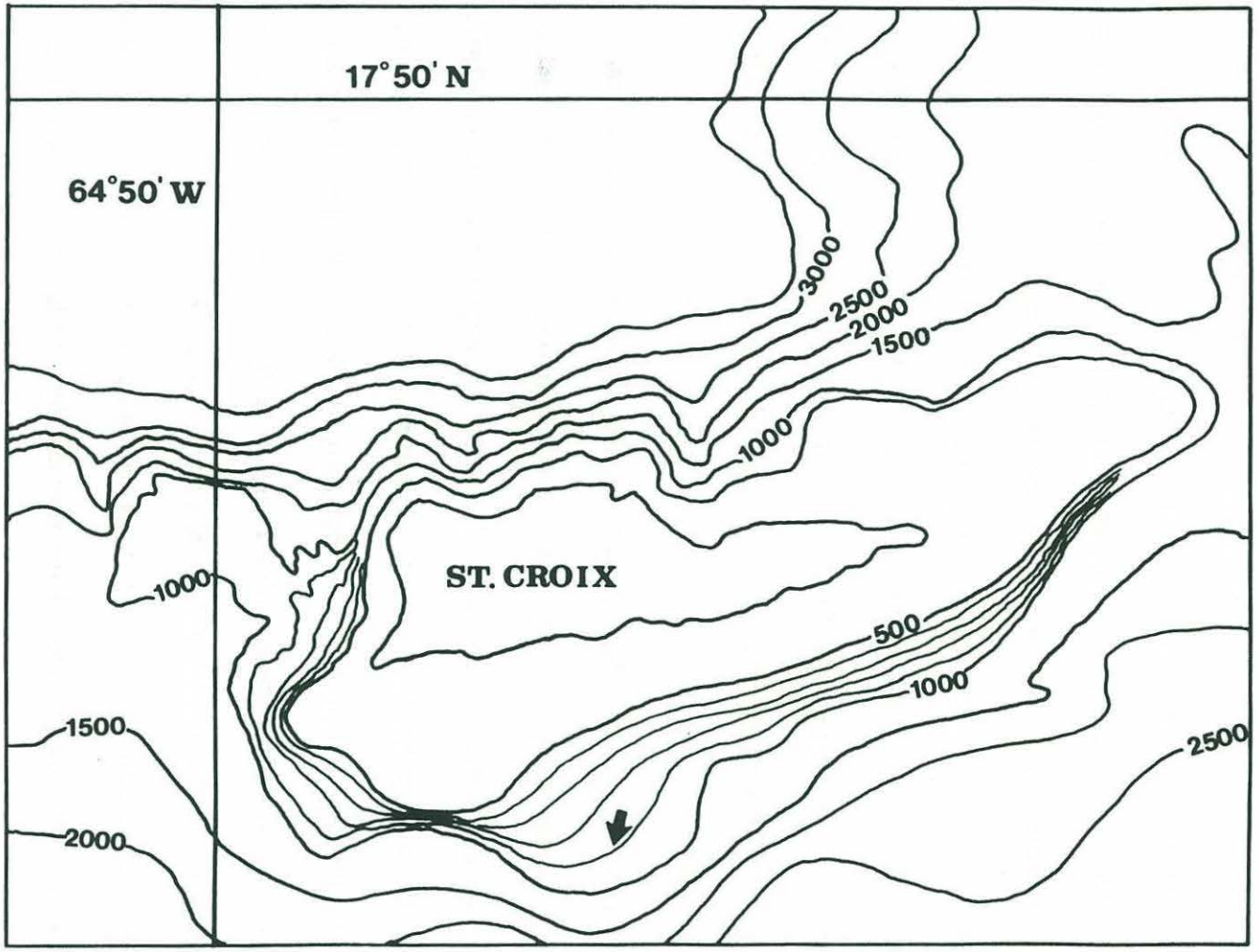


Figure 1 - Chart showing the location of the bottom station in relation to St. Croix, U.S. Virgin Islands. The arrow indicates the specific work area.

submersible work. Bottom currents at the site, though variable, were weak (generally < 5 cm $s^{-1}$ at 5 m above bottom) and directed north and southeast. The bottom sediment was a mixture of fine and very coarse material, composed largely of carbonate tests. Experiments were deployed along a transect, perpendicular to the dominant currents, with depression experiments placed approximately to the west and tray experiments placed approximately to the east of the transponder station marker.

*b. Tray experiments.* Colonization trays (Fig. 2) consisted of a large (40-cm diameter) Delrin plate with a removable cup bolted to its underside (see Snelgrove *et al.* (1992) for a more detailed description of the trays). The cup contained a mesh bag (20-µm opening) that was filled with sediment until the sediment surface was flush with the plate. The sediment in the cup had a surface area of 100 $cm^2$ and a depth of 10 cm. Posts at the periphery of the plate were used to attach the deployment and recovery lids that sealed the trays during transport to and from the bottom. The relatively small area of sediment compared with the large area of the plate was necessary to allow dissipation of the flow disturbance created by the posts at the periphery of the tray, resulting in smooth flow across the surface of the contained sediment. Flume simulations of realistic tray deployments indicated that flow across the sediment surface was very similar to that across the natural bottom (Snelgrove *et al.*, 1992).

Sediment used for all tray experiments was collected on the initial dive at the site using the grab on the manipulator of the submersible. Sediment was defaunated by freezing before it was thawed and added to the trays. Some of the trays (Unenriched Control Trays) were filled with unenriched sediment. Others were organically enriched

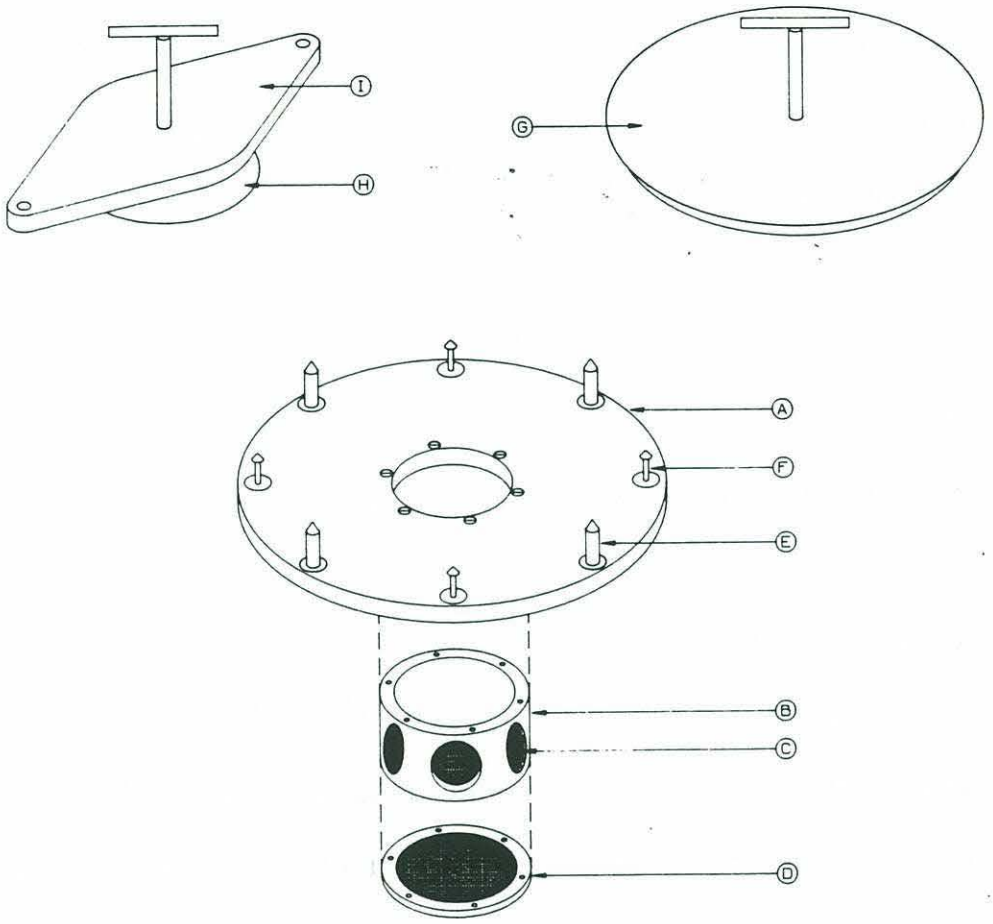


Figure 2 - Side view diagram of colonization tray showing Delrin plastic disk (A), cup (B), mesh bag (C), removable screen bottom (D), guideposts (E), locking pins (F), recovery lid (G), rubber gasket (H), and deployment lid (I). Depth of cup is 10 cm and diameter of disc is 40 cm.

by mixing either ground *Sargassum* sp. (*Sargassum* Trays) or *Thalassiosira* sp. paste (*Thalassiosira* Trays) with the top 2 cm of sediment. *Thalassiosira* sp. paste (Coast Oyster Company, Seattle, no preservative added) was chosen to mimic phytodetritus patches (e.g., Billet *et al.*, 1983), and *Sargassum* sp. was chosen to mimic macroalgal accumulation on the deep-sea floor (e.g., Suchanek *et al.* 1985; Grassle and Morse-Porteous, 1987). *Sargassum* sp. was collected from surface waters off the coast of Florida, and was ground into a mulch to avoid the potential hydrodynamic bias of algae protruding above the sediment surface into the boundary layer. The *Sargassum* Trays and *Thalassiosira* Trays had approximately 1.2% and 1.0% dry weight of organic carbon respectively, and these treatments had substantially more organic content than the ambient sediment (0.7% carbon).

Three trays could be carried on the submersible at one time, therefore one replicate of each of the three treatments was deployed on each dive. The submersible would approach the experimental site from a downcurrent direction; at the site, the manipulating arm of the submersible would excavate a depression in the bottom sediment of approximately the same size and shape as the trays. The manipulator then moved a tray until it was relatively flush with the bottom. Once the bottom current had carried away any resuspended sediment, the deployment lid was carefully removed from the tray and the submersible retreated downcurrent. Although some trays protruded out of the sediment slightly, the flow over the tray was not greatly disrupted (Snelgrove *et al.*, 1992), and these minor flow disturbances were haphazard among treatments. The three trays deployed on a given dive were placed within several meters of each other

in a haphazard sequence along the transect; trays deployed on the subsequent dive were generally placed approximately 10 m further east on the transect. Submersible operators were careful to avoid disturbances that might affect previous deployments. Trays were deployed and recovered in the same sequence, so that all trays remained *in situ* for 23 days. In total, five replicate trays of each treatment were successfully deployed and recovered. One of the *Thalassiosira* Trays was not included in analyses, however, because the tray leaked considerably during transport and had markedly lower faunal densities than the other replicates.

*c. Depression experiments.* Depressions were created with an ALVIN-style box corer (e.g. Grassle and Morse-Porteous, 1987), that encloses an area of 15 x 15 cm and penetrated the St. Croix sediment to approximately 10 cm depth. The depression experiments had the same treatments as the tray experiments; some depressions were unenriched and others were enriched with *Sargassum* sp. or *Thalassiosira* sp. *Sargassum* sp. was added by sealing it inside the benthic grab of the manipulator immediately before the submersible was launched, and then, once on the bottom, opening the grab above a depression immediately after a box core had been taken. *Thalassiosira* sp. was introduced using a device consisting of a sieve with an attached, swivelling wiper blade and T-handle. Algae was smeared over the mesh of the sieve, and the apparatus was sealed in a plastic bag for transport to the bottom. On the bottom, the bag was torn off, and the T-handle turned. This action forced the algae off the sieve into the depression. Aliquots of *Sargassum* sp. and *Thalassiosira* sp. were carefully

preweighed for depression experiments, but some loss always occurred between the time the submersible was launched and algae was added to the depression. Thus, the actual amounts of algae in each depression were unknown. Nevertheless, compared to the ambient environment it represented a substantial organic input. Depression samples reported here are only those where algae was actually seen entering the depression. Macrofaunal response was evaluated by later recoring the depressions with an ALVIN-style box corer. For Unenriched Control Depression 1 and *Sargassum* Depression 1, 25 d passed between the creation and recoring of depressions; for all other depressions, experimental duration was 24 d. On recoring, the box corer consistently penetrated the sediment to at least 4 cm. Four *Sargassum* Depressions, 5 *Thalassiosira* Depressions, and 4 Unenriched Depressions were successfully resampled.

*d. Ambient fauna.* The natural fauna was sampled from the sediment adjacent to tray and depression experiments with an ALVIN-style box corer. Five box cores were taken over undisturbed, flat sediment (hereafter referred to as Flat Ambient), and three box cores were taken over Natural Depressions (approximately 10 cm in diameter and 5 cm deep). Most of the depressions created by taking Flat Ambient box cores were immediately used in the depression experiments described above.

*e. Sample processing.* On board ship, trays and boxcores were carefully extruded at 2-cm vertical intervals and sieved over a 63-μm screen. This screen size was chosen to ensure that juveniles of macrofaunal taxa would be completely enumerated; later

comparison of nested 300 and 63 µm screens indicated that the majority of the fauna was retained on the 300 µm screen. Organisms from both sieve fractions were included in all analyses. Samples were fixed in buffered 4% formaldehyde and transferred to 80% ethanol within a few days. In the laboratory, samples were stained with Rose Bengal and all macrofauna were enumerated under a dissecting microscope. Protozoa and meiofaunal groups such as harpacticoids and nematodes were not counted. Macrofauna were identified to the lowest possible taxon, however, this was often limited by the fact that most specimens were juveniles. Because algal enrichment was either placed on the sediment surface (depressions) or integrated over the top 2 cm of sediment (trays), only individuals from the upper 2 cm of all samples are reported here.

*f. Hypotheses for experiments.* Colonization tray experiments were designed to test the hypothesis that similar densities of similar species would colonize all trays, regardless of amount or type of enrichment, and that this fauna would be comparable to the ambient fauna. Under this null hypothesis, treatments could be similar in densities of individual species, overall faunal composition, or diversity.

Depression experiments were designed to test the same hypothesis, namely that similar faunas would colonize all depression types and that colonizing fauna would not differ from the Flat Ambient fauna. In addition, by comparing results in depressions with those in the colonization trays, it was possible to test the hypothesis that larvae are passively entrained in depressions and should therefore occur in much higher densities in depressions than in trays. Because depression and tray treatments differed in ways

other than flow characteristics, several other hypotheses were tested to explain potential differences between the two types of experiments. Because trays isolated the contained sediment from the surrounding sediment, burrowers and subsurface deposit feeders may have been less abundant in trays than depressions. To test this hypothesis, effects of the treatments in the two types of experiments on the total density of burrowing fauna were qualitatively compared with the effects on non-burrowers. Similarly, the isolation of sediment in trays may exclude subsurface feeders moreso than surface deposit feeders, and higher numbers of subsurface deposit feeders might be expected in depressions than in trays. Because predation may also influence faunal composition, the densities of omnivores (i.e., potential predators) in the different treatments was compared between the two experiments.

Although tray and depression experiments do not directly mimic a natural disturbance, an assumption of these experiments is that natural depressions are a disturbance and may accumulate organic matter, resulting in a patch that a specialized fauna may respond to. Thus, sampling of natural depressions was performed to evaluate whether the fauna in natural depressions differs from that in flat ambient sediment.

*g. Statistical analyses.* For density comparisons, box core surface areas were normalized to the surface area of the colonization trays (100 $cm^2$), therefore densities in colonization trays represent actual counts. Total densities of organisms were compared among depression and tray treatments using the ANOVA model $y = \mu +$ Container + Treatment + Container x Treatment + Error, where $\mu$ is a constant,

Container is the type of experiment (trays or depressions) and Treatment is the amount and type of enrichment (*Thalassiosira*, *Sargassum*, Unenriched Control). All terms in the model were fixed. Data were log (x+1) transformed to homogenize variances. Because the Container x Treatment interaction term was highly significant and the Container and Treatment effects were also significant, the 6 treatments (3 treatments each of trays and depressions) were simultaneously compared with a Tukey's HSD Multiple Comparisons Test to determine which means differed.

Diversity was compared in different treatments using Hurlbert rarefaction (Hurlbert, 1971), a computation of the number of species expected in a random draw of a given number of individuals from a sample. Hurlbert rarefaction is a diversity measure that is sample-size independent, sensitive to rare species (Smith and Grassle, 1977), and the least problematic of the "diversity" measures (Hessler and Jumars, 1974), particularly for deep-sea applications. Hurlbert rarefaction correlates strongly with other diversity measures such as Shannon-Weiner (Grassle and Maciolek, 1992). Replicate samples were pooled to calculate diversity for each of the treatments. Rarefaction curves were calculated for random samples of up to 50 individuals. This number gave the clearest visual representation of the data in a single plot. When the total number of individuals collected was less than 50 for a treatment, abbreviated curves were calculated.

Similarity of samples was measured using the similarity index NESS (Normalized Expected Species Shared) (Grassle and Smith, 1976). The similarity index is based on the number of species two samples would be expected to have in common

if a given number of individuals were randomly drawn from both samples. The NESS values computed for each pair of samples resulted in a similarity matrix that was used in cluster analysis. The clustering package COMPAH90 was used to group samples based on group-average sorting of NESS similarities. Because clustering analysis has several serious drawbacks (e.g., Field *et al.*, 1982), non-metric multidimensional scaling of NESS similarities was also performed. The NESS algorithm requires that the number of randomly chosen individuals must be no more than one half of the smallest number of individuals in any of the samples being compared. Ideally, all of the samples should be included in the analysis, but a compromise was necessary because of variability in the numbers of individuals per sample. Therefore, a random draw of 9 individuals was used for comparison of samples; this choice allowed inclusion of all samples but the Unenriched Control Trays. Although a random draw of 9 individuals would often be inadequate for comparison of shallow-water samples where several species often dominate, we felt it was sufficient for deep-sea samples because rare species are a significant fraction of the total species pool. Indeed, comparisons based on a larger number of individuals revealed similar groupings for those samples that had sufficient numbers of individuals to be included in the analysis.

To evaluate the importance of isolation of trays from the surrounding sediment (i.e., organisms had to enter trays from the surface and could not burrow in from the sides) and clarify potential differences between depression and tray fauna, comparisons were made between tray treatments and corresponding depression treatments of total numbers of surface deposit feeders, subsurface deposit feeders and potential carnivores,

and burrowing versus non-burrowing fauna. Substantially fewer individuals were also collected in depressions compared with trays (see Results), and one possible explanation for this pattern is that carnivores were more able to colonize depressions than trays, and thus reduce total densities of organisms in depressions. Classifying organisms into different feeding and mobility groups proved to be a difficult task, and reliable classifications were readily available only for polychaetes (from Fauchald and Jumars, 1979). Thus, only polychaetes were categorized and analyzed in this manner, although this includes the majority of individuals sampled. Nevertheless, these classifications are tentative, particularly given the flow-dependent behavior that has recently been demonstrated for some species (e.g. Taghon *et al.*, 1980; Miller *et al.*, in press). In classifying polychaetes into feeding modes, it was impossible to discern whether omnivores such as hesionids might be carnivores; therefore, omnivores were included with carnivores based on the assumption that they are potentially carnivorous. To establish whether differences in mobility of trophic groups might be attributed to one of two abundant polychaete taxa (*Capitella* spp. and *Nereimyra* sp.), these taxa were compared across treatments (*Thalassiosira*, *Sargassum*, Unenriched Controls) and container type (trays or depressions), however, Unenriched Control Trays and Unenriched Control Depressions were dropped from the analysis because densities of each replicate were often all or nearly all zeroes, resulting in extremely low or zero variance.

In separate analyses, differences in mobility, trophic mode, and dominant polychaetes were initially tested using the ANOVA model, $y = \mu + \text{Container} +$

Treatment + Container x Treatment + Error, where μ is a constant, Container is the type of experiment (trays or depressions) and Treatment is amount and type of enrichment (*Thalassiosira, Sargassum,* Unenriched Control). All terms in the model were fixed. In all cases, data were log (x+1) transformed to homogenize variances. For all between-treatment comparisons made (burrowers, non-burrowers, omnivores, surface deposit feeders, subsurface deposit feeders, *Capitella* spp. and *Nereimyra* sp.) the Container x Treatment interaction term was highly significant, therefore when the Treatment or Container effect was significant, the 6 treatments (3 treatments each of trays and depressions) were simultaneously compared with Tukey's HSD Multiple Comparisons Tests to determine which means differed. An assumption of this analysis is that the potentially confounding effect of location of trays and depressions was unimportant (i.e., the placement of tray experiments several hundred yards away from depression experiments did not contribute to differences between trays and depressions).

## 3. Results

Although ambient densities of organisms were somewhat low compared with many deep-sea habitats (reviewed in Grassle and Morse-Porteous, 1987), a large number and broad diversity of organisms colonized different treatments over the relatively short time scale of the experiment (Table 1). In total, 4101 individuals colonized artificial treatments, representing 117 different taxa.

Comparisons of total densities for different treatments revealed several very striking patterns (Fig. 3). Enriched trays had significantly higher total densities than any

Table 1. Total numbers of macrofaunal organisms in Sediment Tray and Artificial Depression treatments as well as total numbers of macrofauna in samples from ambient flat areas and natural depressions. Trophic modes and motility are given for polychaete taxa. SDF denotes surface deposit feeder, SSDF denotes subsurface deposit feeder, F denotes filter feeders, C denotes carnivores and O denotes omnivores. For motility, organisms are divided into burrowers (B) and non-burrowers (N). Within treatments, Thal denotes *Thalassiosira* enrichments, Sarg denotes *Sargassum* enrichments, and Cont denotes Unenriched treatments. Ambient fauna was sampled over flat (Flat) areas and natural depressions (Dep). Numbers below treatments indicate numbers of replicates.

| Taxon | Family | Trophic Mode | Motile? | Sediment Trays | | | Depressions | | | Ambient | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | Thal (4) | Sarg (5) | Cont (5) | Thal (5) | Sarg (4) | Cont (4) | Flat (5) | Dep (3) |
| **Polychaetes** | | | | | | | | | | | |
| Acrocirridae | Acrocirridae | SDF | N | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 5 |
| Ampharetidae | Ampharetidae | SDF | N | 110 | 7 | 0 | 0 | 6 | 4 | 3 | 0 |
| *Amphicteis vestis* | Ampharetidae | SDF | N | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| *Anobothrus gracilis* | Ampharetidae | SDF | N | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Aonidella* sp. | Spionidae | SDF | N | 0 | 0 | 2 | 0 | 0 | 1 | 1 | 0 |
| *Aphelochaeta marioni* | Cirratulidae | SDF | N | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 1 |
| *Apistobranchus* spp. | Apistobranchidae | SDF | N | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Aricidea abranchitata* | Paraonidae | SDF | B | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *A. cerrutii* | Paraonidae | SDF | B | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 |
| *A. simplex* | Paraonidae | SDF | B | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 0 |
| *Aricidea* spp. | Paraonidae | SDF | B | 0 | 0 | 0 | 3 | 1 | 1 | 7 | 2 |
| *A. tetrabranchia* | Paraonidae | SDF | B | 0 | 0 | 0 | 2 | 1 | 0 | 2 | 3 |
| *A. wassi* | Paraonidae | SDF | B | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 |
| *Aurospio dibranchiata* | Spionidae | SDF | N | 0 | 0 | 0 | 17 | 4 | 9 | 21 | 11 |

Table 1 (cont.)

| Taxon | Family | Trophic Mode | Motile? | Sediment Trays | | | Depressions | | | Ambient | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | Thal (4) | Sarg (5) | Cont (5) | Thal (5) | Sarg (4) | Cont (4) | Flat (5) | Dep (3) |
| *Axiokebuita millsi* | Scalibregmidae | SSDF | B | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 |
| *Braniella* sp. | Syllidae | C | N | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| *Capitella* spp. | Capitellidae | SSDF | B | 916 | 399 | 1 | 1 | 150 | 0 | 1 | 2 |
| *Ceratocephale pacifica* | Nereidae | O | N | 0 | 0 | 0 | 4 | 1 | 1 | 5 | 4 |
| *Chaetozone setosa* | Cirratulidae | SDF | N | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| Chrysopetalidae spp. | Chrysopetalidae | C | B | 22 | 0 | 0 | 1 | 1 | 0 | 0 | 3 |
| Cirratulidae sp. | Cirratulidae | SDF | N | 0 | 0 | 1 | 1 | 2 | 2 | 1 | 6 |
| *Diplocirrus* sp. | Flabelligeridae | SSDF | B | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| Dorvilleidae sp. | Dorvilleidae | O | B | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 |
| *Dysponetus* sp. | Chrysopetalidae | C | B | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 |
| *Euchone incolor* | Sabellidae | F | N | 0 | 0 | 0 | 1 | 1 | 1 | 3 | 0 |
| *E. scotiarum* | Sabellidae | F | N | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *Eunice pennata* | Eunidicae | C | B | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 |
| *Exogone* sp. | Syllidae | O | N | 0 | 0 | 1 | 1 | 2 | 2 | 10 | 1 |
| *Fabricia* sp. | Sabellidae | F | N | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| *Fauveliopsis* sp. | Fauveliopsidae | SSDF | B | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 |
| *Flabelligella* sp. | Flabelligeridae | SDF | N | 0 | 0 | 0 | 0 | 0 | 1 | 3 | 0 |
| Flabelligeridae sp. | Flabelligeridae | SDF | N | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 |
| *Glycera* | Glyceridae | C | B | 0 | 0 | 1 | 3 | 4 | 5 | 4 | 3 |

Table 1 (cont.)

| Taxon | Family | Trophic Mode | Motile? | Sediment Trays | | | Depressions | | | Ambient | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | Thal (4) | Sarg (5) | Cont (5) | Thal (5) | Sarg (4) | Cont (4) | Flat (5) | Dep (3) |
| Goniadidae sp. | Goniadidae | C | B | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| *Harmothoe* sp. | Polynoidae | C | N | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| Hesionidae sp. 1 | Hesionidae | O | B | 4 | 25 | 0 | 3 | 5 | 3 | 1 | 0 |
| Hesionidae sp. 2 | Hesionidae | O | B | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| Hesionidae sp. 3 | Hesionidae | O | B | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 9 |
| *Hesiospina similis* | Hesionidae | O | B | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| *Jasmineira* | Sabellidae | F | N | 0 | 0 | 0 | 1 | 1 | 2 | 1 | 0 |
| *Laonice* sp. | Spionidae | SDF | N | 9 | 20 | 1 | 1 | 5 | 1 | 1 | 0 |
| *Levinsenia flava* | Paraonidae | SDF | B | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| *Levinsenia uncinata* | Paraonidae | SDF | B | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 0 |
| Lumbrineridae sp. | Lumbrineridae | O | B | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| *Lumbrinerinides carpinei* | Lumbrineridae | O | B | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *Lumbrineris latreilli* | Lumbrineridae | O | B | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 |
| *Monticellina* sp. | Cirratulidae | SDF | N | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 |
| *Neanthes* sp. | Nereidae | O | N | 3 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| Nereididae sp. | Nereididae | O | N | 19 | 6 | 1 | 2 | 1 | 1 | 0 | 0 |
| *Nereimyra punctata* | Hesionidae | O | B | 509 | 241 | 0 | 1 | 50 | 2 | 0 | 3 |
| *Nothria* sp. | Onuphidae | O | N | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Notomastus lacericeus* | Capitellidae | SSDF | B | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 |

Table 1 (cont.)

| Taxon | Family | Trophic Mode | Motile? | Sediment Trays | | | Depressions | | | Ambient | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | Thal (4) | Sarg (5) | Cont (5) | Thal (5) | Sarg (4) | Cont (4) | Flat (5) | Dep (3) |
| *Notomastus* sp. | Capitellidae | SSDF | B | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Oligobregma* sp. | Scalibregmidae | SSDF | B | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 |
| Onuphidae sp. | Onuphidae | O | N | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| Ophelidae sp. | Ophelidae | SSDF | B | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| *Ophelina abranchiata* | Opheliidae | SSDF | B | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *O. cylinidricaudata* | Opheliidae | SSDF | B | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 |
| *Ophelina aulogastrella* | Opheliidae | SSDF | B | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *Ophryotrocha maciolekae* | Dorvilleidae | O | B | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *Ophryotrocha* sp. 1 | Dorvilleidae | O | B | 1 | 2 | 0 | 0 | 3 | 0 | 0 | 0 |
| *Ophryotrocha* sp. 2 | Dorvilleidae | O | B | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Orbiniella* sp. | Orbiniidae | SSDF | B | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 |
| Oweniidae sp. | Oweniidae | SDF | N | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 |
| Paraonidae sp. | Paraonidae | SSDF | B | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 |
| *Paraonella* sp. | Paraonidae | SDF | B | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *Paraonis* sp. nov. | Paraonidae | SDF | B | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 |
| *Pettiboneia bathyalis* | Phyllodocidae | O | B | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *Pholoe anoculata* | Pholoididae | C | B | 5 | 1 | 0 | 6 | 3 | 1 | 10 | 1 |
| Pilargidae gen. nov. | Pilargidae | C | B | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| Phyllodocidae sp. | Phyllodocidae | O | B | 0 | 0 | 0 | 1 | 1 | 2 | 0 | 3 |

Table 1 (cont.)

| Taxon | Family | Trophic Mode | Motile? | Sediment Trays | | | Depressions | | | Ambient | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | Thal (4) | Sarg (5) | Cont (5) | Thal (5) | Sarg (4) | Cont (4) | Flat (5) | Dep (3) |
| *Poecilochaetus* sp. | Poecilochaetidae | SDF | N | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 |
| *Polycirrus* sp. | Terebellidae | SDF | N | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| Polynoidae sp. | Polynoidae | O | N | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 2 |
| *Prionospio* sp. | Spionidae | SDF | N | 0 | 0 | 0 | 0 | 3 | 1 | 1 | 3 |
| *Protodorvillea* sp. | Dorvilleidae | O | B | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *Protomystides* sp. | Phyllodocidae | O | B | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 4 |
| *Pseudoscalibregma parvum* | Scalibregmidae | SSDF | B | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 |
| Sabellidae sp. | Sabellidae | F | N | 0 | 0 | 0 | 3 | 2 | 1 | 7 | 2 |
| *Sarsonuphis* sp. | Onuphidae | O | B | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 |
| Serpulidae sp. | Serpulidae | SDF | N | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| Sigalionidae sp. | Sigalionidae | O | B | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| Sphaerodoridae sp. | Sphaerodiridae | SDF | N | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| Spionidae spp. | Spionidae | SDF | N | 0 | 0 | 4 | 7 | 4 | 7 | 9 | 3 |
| *Spiophanes* sp. | Spionidae | SDF | N | 0 | 0 | 0 | 1 | 2 | 2 | 11 | 2 |
| Syllidae sp. | Syllidae | C | N | 0 | 0 | 0 | 4 | 1 | 1 | 2 | 1 |
| *Terebellides* sp. | Terebellidae | SDF | N | 0 | 0 | 2 | 0 | 1 | 2 | 1 | 0 |
| *Tharyx* sp. | Cirratulidae | SDF | N | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 |
| *Therochaeta* sp. | Flabelligeridae | SDF | N | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| Trichobranchidae sp. | Trichobranchidae | SDF | N | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 2 |

Table 1 (cont.)

| Taxon | Family | Trophic Mode | Motile? | Sediment Trays | | | Depressions | | | Ambient | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | Thal (4) | Sarg (5) | Cont (5) | Thal (5) | Sarg (4) | Cont (4) | Flat (5) | Dep (3) |
| Trochochaeta sp. | Trochochaetidae | SDF | N | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| Polychaete larvae | | | | 20 | 0 | 1 | 9 | 2 | 1 | 2 | 5 |
| Misc. Polychaetes | | | | 0 | 0 | 0 | 0 | 1 | 0 | 5 | 3 |
| **Oligochaetes** | | | | | | | | | | | |
| *Bathydrilus* sp. | Tubificidae | | | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 |
| *Grania* sp. | Enchytraetidae | | | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 |
| *Phallodrilus* sp. | Tubificidae | | | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| Tubificidae sp. | Tubificidae | | | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 |
| **Crustaceans** | | | | | | | | | | | |
| *Abyssijaera* sp. | Janiridae | | | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Agathotanais* sp. | Anarthruridae | | | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| Akanthophoreinae | Anarthruridae | | | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| Ampeliscidae sp. | Ampeliscidae | | | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *Atlantapseudes* sp. | Apseudidae | | | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *Chelator* sp. | Desmosomatidae | | | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| *Collettea* sp. | Anarthruridae | | | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Cumella* sp. | Nannastacidae | | | 858 | 78 | 2 | 0 | 25 | 0 | 2 | 4 |
| *Cumella* sp. II | Nannastacidae | | | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 |
| Decapoda sp. I | Undet. | | | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |

Table 1 (cont.)

| Taxon | Family | Trophic Mode | Motile? | Sediment Trays | | | Depressions | | | Ambient | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | Thal (4) | Sarg (5) | Cont (5) | Thal (5) | Sarg (4) | Cont (4) | Flat (5) | Dep (3) |
| Decapoda sp. II | | | | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| Desmosomatidae | Desmosomatidae | | | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 |
| *Disconectes* sp. 1 | Eurycopidae | | | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 |
| *Disconectes* sp. 2 | Eurycopidae | | | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 |
| *Dyopedos* sp. | Dulichiidae | | | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *Eugerda* sp. | Desmosomatidae | | | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Eurycope* sp. | Eurycopidae | | | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *Eusiris* sp. | Eusiridae | | | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 |
| Gammaridae sp. | Gammaridae | | | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 |
| Gnathiidae sp. | Gnathiidae | | | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Haplocope* sp. | Anarthruridae | | | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| *Harpinia* sp. | Phoxocephalidae | | | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 |
| Haustoriidae sp. | Haustoriidae | | | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *Ilyarachna* sp. | Ilyarachnidae | | | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| Ilyarachnidae sp. | Ilyarachnidae | | | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| *Ischyrocerus* sp. | Podoceridae | | | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 |
| Ishnomesidae sp. | Ishnomesidae | | | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| Janiridae sp. | Janiridae | | | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *Lipomera* sp. | Eurycopidae | | | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |

Table 1 (cont.)

| Taxon | Family | Trophic Mode | Motile? | Sediment Trays | | | Depressions | | | Ambient | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | Thal (4) | Sarg (5) | Cont (5) | Thal (5) | Sarg (4) | Cont (4) | Flat (5) | Dep (3) |
| Leptognathiinae sp. 1 | Anarthruridae | | | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| Leptognathiinae sp. 2 | Anarthruridae | | | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| Lysianassidae sp. 1 | Lysianassidae | | | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 |
| Lysianassidae sp. 2 | Lysianassidae | | | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| Lysianassidae sp. 3 | Lysianassidae | | | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| Lysianassidae sp. 4 | Lysianassidae | | | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| Munnopsidae sp. | Munnopsidae | | | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| Mysidacea | Undet. | | | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| Nannoniscidae | n. gen. n. sp. | | | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 |
| *Nannoniscus* sp. 1 | Desmosomatidae | | | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| *Nannoniscus* sp. 2 | Desmosomatidae | | | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| *Nebalia* sp. | Nebaliidae | | | 182 | 9 | 1 | 0 | 101 | 1 | 0 | 0 |
| *Neotanais* sp. nov. | Neotanaidae | | | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| Oedicerotidae sp. | Oedicerotidae | | | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| *Panetela* sp. | Nannoniscidae | | | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 |
| *Peraeospinosus* sp. | Typhlotanaidae | | | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| *Paranarthrura* sp. | Anarthruridae | | | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *Paraphoxus* sp. | Phoxocephalidae | | | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| *Paratyphlotanais* sp. | Typhlotanaidae | | | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |

Table 1 (cont.)

| Taxon | Family | Trophic Mode | Motile? | Sediment Trays | | | Depressions | | | Ambient | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | Thal (4) | Sarg (5) | Cont (5) | Thal (5) | Sarg (4) | Cont (4) | Flat (5) | Dep (3) |
| *Phoxocephalus* sp. | Phoxocephalidae | | | 0 | 0 | 0 | 1 | 0 | 0 | 3 | 0 |
| *Pleurogonium* sp. | Munnidae | | | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *Prochelator* sp. | Desmosomatidae | | | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| *Pseudoleptochelia* sp. | Leptocheliidae | | | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Pseudotanais* sp. 1 | Pseudotanaidae | | | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 |
| *Synchelidium* sp. | Oedicerotidae | | | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 |
| Typhlotanaidae | Typhlotanaidae | | | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *Whoia* sp. | Desmosomatidae | | | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| **Molluscs** | | | | | | | | | | | |
| Bivalve sp. 1 | | | | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| Bivalve sp. 2 | | | | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 1 |
| Bivalve sp. 3 | | | | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| Bivalve sp. 4 | | | | 0 | 0 | 0 | 1 | 3 | 1 | 0 | 4 |
| Bivalve sp. 5 | | | | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 |
| Bivalve sp. 6 | | | | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| Bivalve sp. 7 | | | | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 |
| Bivalve sp. 8 | | | | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| Bivalve sp. 9 | | | | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| Gastropod sp. I | | | | 0 | 0 | 0 | 1 | 3 | 1 | 0 | 2 |

Table 1 (cont.)

| Taxon | Family | Trophic Mode | Motile? | Sediment Trays | | | Depressions | | | Ambient | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | Thal (4) | Sarg (5) | Cont (5) | Thal (5) | Sarg (4) | Cont (4) | Flat (5) | Dep (3) |
| Gastropod sp. II | | | | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| Gastropod sp. III | | | | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| Gastropod sp. IV | | | | 0 | 0 | 0 | 0 | 0 | 3 | 1 | 0 |
| Gastropod sp. V | | | | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| Neomeniomorpha sp. 1 | | | | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| Neomeniomorpha sp. 2 | | | | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| Neomeniomorpha sp. 3 | | | | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| Neomeniomorpha sp. 4 | | | | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 |
| Neomeniomorpha sp. 5 | | | | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| Neomeniomorpha sp. 6 | | | | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 |
| Scaphopoda sp. 1 | | | | 0 | 0 | 2 | 0 | 1 | 1 | 0 | 0 |
| Scaphopoda sp. 2 | | | | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 2 |
| Scaphopoda sp. 3 | | | | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| Scaphopoda sp. 4 | | | | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 |
| Scaphopoda sp. 5 | | | | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| Prochaetodermatidae | Prochaetodermatidae | | | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| **Echinoderms** | | | | | | | | | | | |
| Holothurian | | | | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| Ophiuroid 1 | | | | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 |

Table 1 (cont.)

| Taxon | Family | Trophic Mode | Motile? | Sediment Trays | | | Depressions | | | Ambient | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | Thal (4) | Sarg (5) | Cont (5) | Thal (5) | Sarg (4) | Cont (4) | Flat (5) | Dep (3) |
| Ophiuroid 2 | | | | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| Ophiuroid 3 | | | | 0 | 0 | 0 | 0 | 0 | 0 | 6 | 2 |
| Ophiuroid 4 | | | | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| Ophiuroid 5 | | | | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| Echiuran | | | | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| *Aspidosiphon* sp. | | | | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Phascolosoma* sp. | | | | 0 | 1 | 0 | 0 | 2 | 0 | 4 | 0 |
| Nemertinea spp. | | | | 0 | 1 | 0 | 4 | 0 | 2 | 4 | 6 |

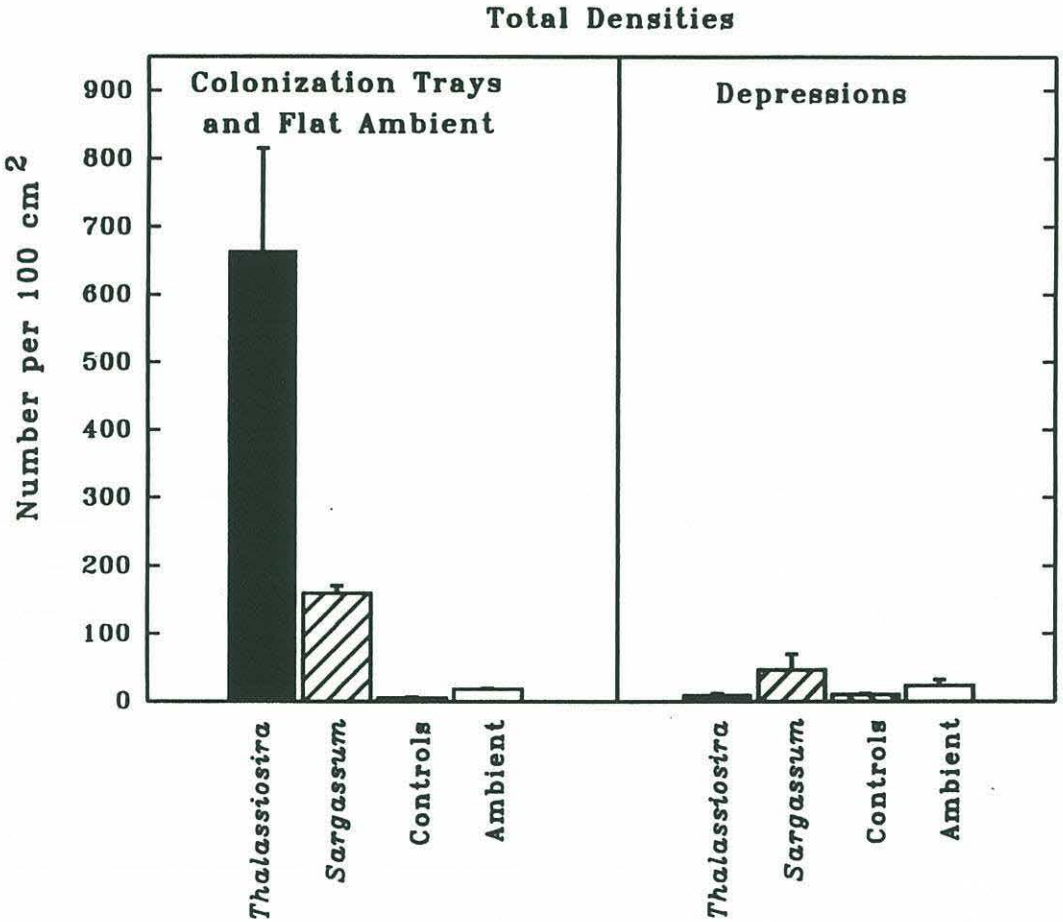


Figure 3 - Densities of all macrofauna combined for *Thalassiosira* Trays (n=4), *Thalassiosira* Depressions (n=5), *Sargassum* Trays (n = 5), *Sargassum* Depressions (n = 4), Control Trays (n=5), Control Depressions (n=4), Ambient Flat sediment (n=5), and Natural Depressions (n=3). Bars denote mean values and lines denote 1 standard error.

of the other treatments, and numbers greatly exceeded those in the ambient sediment. *Thalassiosira* Trays had significantly higher numbers of animals than any other treatment. Unenriched Control Trays were colonized by very few individuals, and mean densities were far less than that in the ambient sediment.

Results for depressions were very different from those for trays. Mean total densities were highest in *Sargassum* Depressions compared with *Thalassiosira* and Unenriched Control Depressions, however, none of the depression treatments were significantly different (Table 2). Neither *Thalassiosira* Depressions nor Unenriched Control Depressions exceeded ambient faunal densities. Although mean values for total densities in all 3 types of artificial depression were slightly higher than in Unenriched Control Trays, densities were much lower than in enriched trays. Densities in *Sargassum* Depressions were significantly higher than Unenriched Control Trays. Total densities in Natural Depressions were comparable to Ambient Flat samples. Because the four most abundant colonizers (*Capitella* spp., *Nereimyra* sp., *Nebalia* sp., and *Cumella* sp.) comprised approximately 86% of the total individuals collected in tray and depression experiments, it is not surprising that patterns of colonization for these taxa (Fig. 4) were similar to those observed for combined totals (Fig. 3). *Capitella* spp., *Nereimyra* sp., and *Cumella* sp. were all extremely abundant in *Thalassiosira* Trays, moderately abundant in *Sargassum* Trays, less abundant in *Sargassum* Depressions, and virtually absent from *Thalassiosira* Depressions. All of these species were rare or absent from Unenriched Control Trays, Unenriched Control Depressions and Flat Ambient samples. *Nebalia* sp. was the only abundant colonizer that had higher mean

Table 2. ANOVA results for total densities of organisms in Depression and Tray experiments. Total densities were compared between Container types (Trays and Depressions) and Treatments (*Thalassiosira, Sargassum,* Controls). Data were log (x+1) transformed to homogenize variances. Means were compared with a Tukey's Multiple Comparisons Test.

| Source | df | SS | F | p |
|---|---|---|---|---|
| Container | 1 | 18.236 | 63.897 | 0.000 |
| Treatment | 2 | 15.582 | 54.598 | 0.000 |
| Container x Treatment | 2 | 12.624 | 44.233 | 0.000 |
| Error | 21 | 0.285 | | |



| Treatment Mean | *Thalassiosira* Trays | *Sargassum* Trays | *Sargassum* Depressions | Control Depressions | *Thalassiosira* Depressions | Control Trays |
|---|---|---|---|---|---|---|
| | 664.5 | 159.8 | 46.2 | 10.2 | 9.86 | 5.0 |

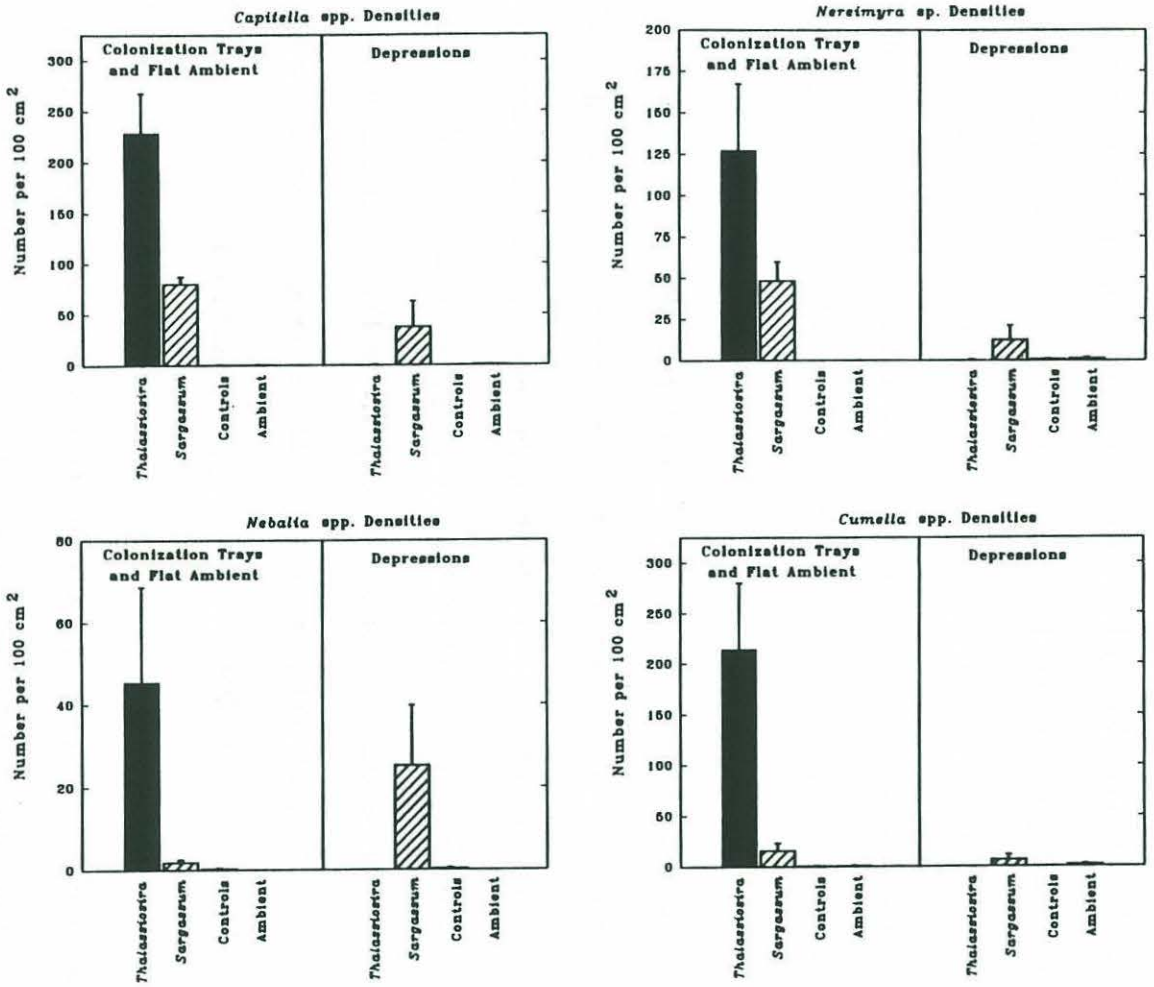


Figure 4 - Densities of the four most abundant taxa of colonizers in colonization trays, artificial and natural depressions and ambient fauna. See caption of Fig. 3 for number of replicates for each treatment. Bars denote mean values and lines denote 1 standard error.

density in a depression treatment (*Sargassum*) compared with a similar tray treatment, however, the variance was very high and colonization of *Thalassiosira* Trays for this species was substantially higher than *Thalassiosira* Depressions. *Nebalia* sp. densities in Unenriched Control Trays and Unenriched Control Depressions was extremely low. In summary, total densities and densities of dominant taxa in depression treatments were either comparable to or considerably lower than in corresponding tray treatments.

The two major groups in the clustering analysis (Fig. 5) included enriched trays and *Sargassum* Depressions in one group and depression treatments and ambient samples in a second group. The relationship between depression treatments and the ambient fauna is more easily discerned in the multidimensional scaling (MDS) analysis of NESS values (Fig. 6), where representation of data similarity is not limited to two dimensions. The 3-dimensional MDS gave a shear value of 0.085 (0.1 is considered a maximum acceptable stress level, E.D. Gallagher, pers. comm.). In dimensions 1 and 2, the pattern is quite similar to that observed in the clustering analysis. *Sargassum* Trays and *Thalassiosira* Trays form a tight grouping separate from Flat Ambient fauna and most artificial depressions. Only *Sargassum* Depressions have a faunal affinity with enriched trays. Other depression treatments are weakly separated from one another and from Flat Ambient Fauna. In dimensions 1 and 2, Flat Ambient fauna overlaps with *Thalassiosira* Depressions, and to a lesser degree with Unenriched Control Depressions. In dimensions 1 and 3, however, *Thalassiosira* Depressions show modest separation from Flat Ambient fauna and some overlap with Unenriched Control Depressions. In dimensions 1 and 2, Natural Depressions are widely scattered, however, in dimensions

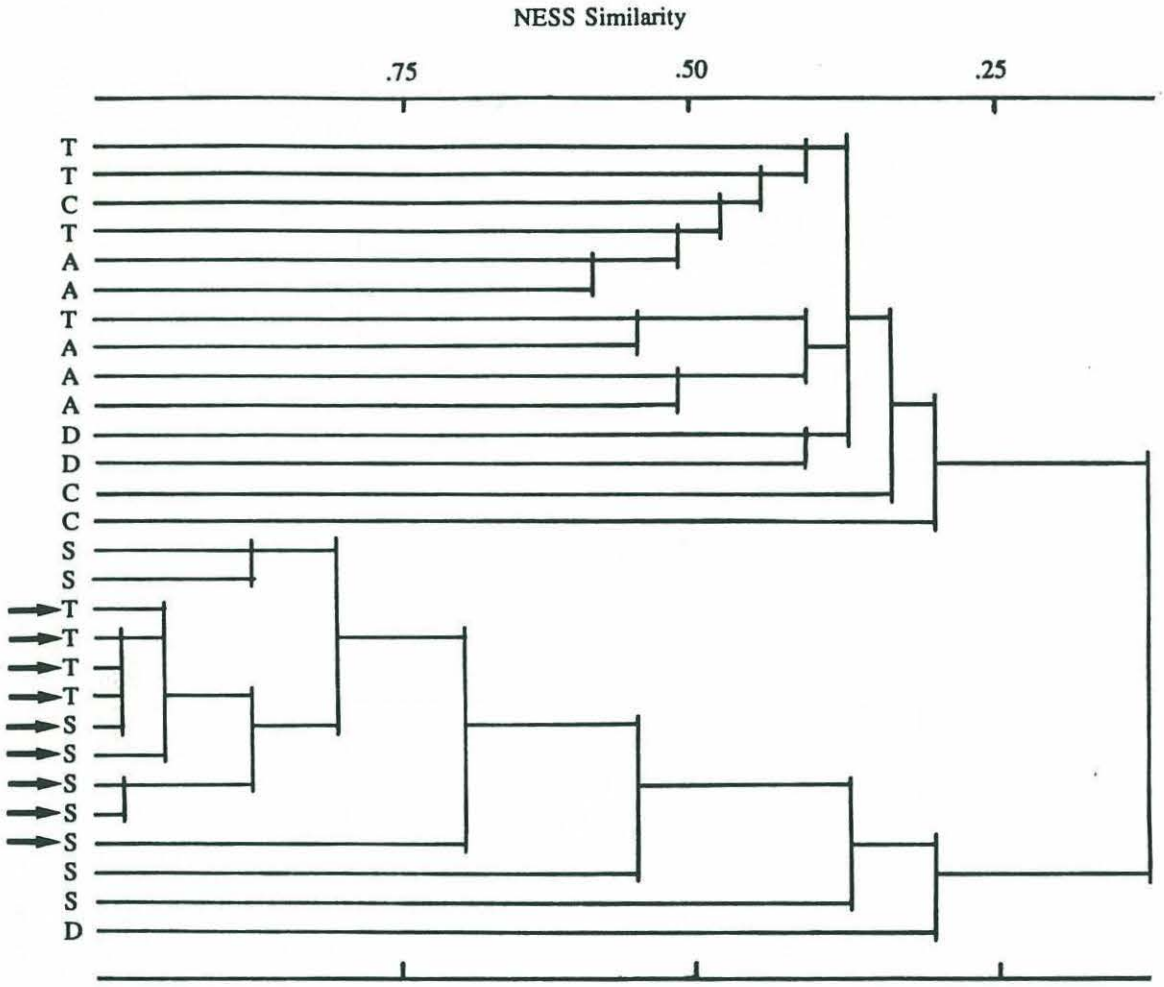


Figure 5 - Clustering of individual samples based on group-average sorting of NESS (Normalized Expected Species Shared) similarities with a random draw of 9 individuals per sample. "T" denotes *Thalassiosira* Trays and Depressions, "S" denotes *Sargassum* Trays and Depressions, "C" denotes Control Depressions, "D" denotes Natural Depressions, and "A" denotes Ambient fauna. Arrows indicate Trays. Control Trays were not included in the analysis because all of the replicates contained less than 18 individuals (see Materials and Methods).

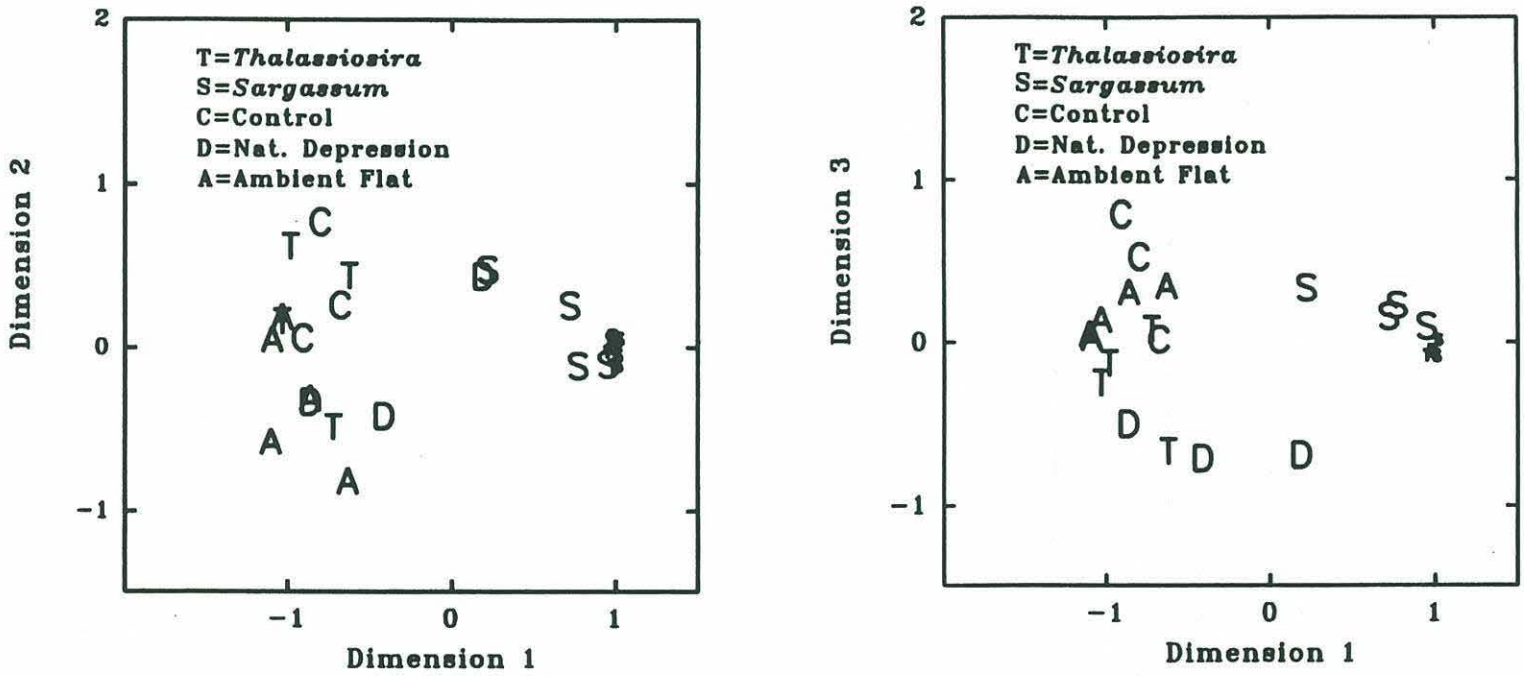


Figure 6 - Nonmetric multidimensional scaling of individual samples based on NESS (Normalized Expected Species Shared) similarities with a random draw of 9 individuals per sample. *Thalassiosira* Trays and *Sargassum* Trays in smaller letters on the far right of each plot, and Control Trays were not included in the analysis (see Materials and Methods). A three-dimensional plot was found to provide a reasonable representation of the data, however, the plot of dimension 2 and dimension 3 is not shown because it added no additional information to the plots shown.

1 and 3 they clearly separate from Flat Ambient fauna and have modest affinity with *Thalassiosira* Depressions. In summary, enriched trays, *Sargassum* Depressions and Natural Depressions all have somewhat unique faunas, and *Thalassiosira* Depressions, Unenriched Control Depressions and Flat Ambient fauna show very weak separation.

Hurlbert rarefaction indicated very reduced diversity in enriched trays, and modestly reduced diversity in *Sargassum* Depressions (Fig. 7). Diversity in *Sargassum* Trays was substantially higher than in *Thalassiosira* Trays (Snelgrove *et al.*, 1992), but only when comparing very large numbers of individuals. Nonetheless, of the tray treatments, only Unenriched Control Trays were as diverse as artificial depressions and ambient fauna. Unenriched Control Depressions, Unenriched Control Trays and Natural Depressions all had similar high diversity, and *Thalassiosira* Depression diversity was only slightly reduced. Thus, there is little evidence for reduced diversities resulting from these artificial (*Thalassiosira* Depressions, Unenriched Control Depressions and Unenriched Control Trays) and natural (Natural Depressions) "patches" of disturbance.

Colonization trays may have attracted non-burrowing fauna but isolated burrowing fauna (e.g., Kukert and Smith, 1992). Analysis of variance indicated that non-burrowers were more abundant in enriched trays than enriched depressions (Table 3), however, Unenriched Control Depressions and Unenriched Control Trays did not differ. For burrowers, Unenriched Control Depressions and Unenriched Control Trays were the only case where corresponding tray and depression treatments significantly differed; significantly fewer burrowers were observed in Unenriched Control Trays. These results suggest that trays may have deterred burrowers, although the two most

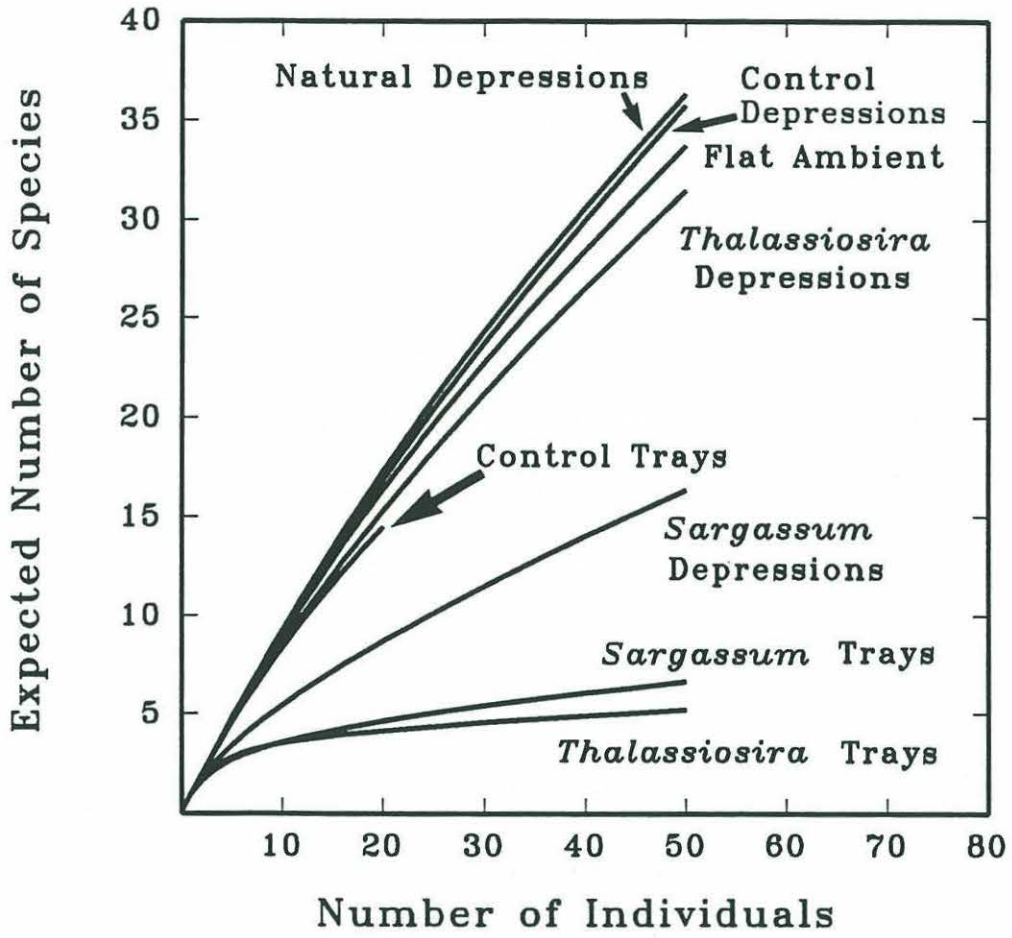


Figure 7 - Number of individuals plotted against Expected Species (Hurlbert rarefaction) for each tray and depression treatment and Flat Ambient and Natural Depression samples. Each curve is based on combined replicates of each treatment. The curve for Control Trays is abbreviated because so few individuals were sampled.

Table 3. ANOVA results for Depression and Tray Experiments[α]. Motility and feeding types (see Table 1) for polychaetes were compared between treatments (*Thalassiosira*, *Sargassum*, Controls) and Containers (Trays and Depressions). The two abundant polychaete taxa (*Capitella* spp. and *Nereimyra* sp.) were also compared between treatments[β]. Where significant differences were observed, treatment means were compared with Tukey's Multiple Comparisons Tests.

| Source | df | SS | F | *p* |
|---|---|---|---|---|
| **Burrowers** | | | | |
| Container | 1 | 0.310 | 0.860 | 0.364 |
| Treatment | 2 | 4.771 | 6.627 | 0.006** |
| Container x Treatment | 2 | 5.933 | 8.241 | 0.002** |
| Error | 21 | 7.559 | | |

| Treatment | *Thalassiosira* Trays | *Sargassum* Depressions | Control Depressions | *Thalassiosira* Depressions | *Sargassum* Trays | Control Trays |
|---|---|---|---|---|---|---|
| Mean | 35.25 | 10.00 | 10.05 | 9.00 | 7.00 | 2.80 |

| Source | df | SS | F | *p* |
|---|---|---|---|---|
| **Non-burrowers** | | | | |
| Container | 1 | 12.243 | 30.899 | 0.000*** |
| Treatment | 2 | 51.553 | 65.053 | 0.000*** |
| Container x Treatment | 2 | 26.283 | 33.165 | 0.000*** |
| Error | 21 | 8.32 | | |

Table 3 (cont.)

| Treatment | *Thalassiosira* Trays | *Sargassum* Trays | *Sargassum* Depressions | *Thalassiosira* Depressions | Control Depressions | Control Trays |
|---|---|---|---|---|---|---|
| Mean | 364.25 | 133.8 | 55.75 | 7.2 | 5.25 | 1.0 |

| Source | df | SS | F | *p* |
|---|---|---|---|---|
| **Omnivores** | | | | |
| Container | 1 | 7.904 | 18.655 | 0.000*** |
| Treatment | 2 | 30.769 | 36.311 | 0.000*** |
| Container x Treatment | 2 | 16.520 | 19.496 | 0.000*** |
| Error | 21 | 8.897 | | |

| Treatment | *Thalassiosira* Trays | *Sargassum* Trays | *Sargassum* Depressions | *Thalassiosira* Depressions | Control Depressions | Control Trays |
|---|---|---|---|---|---|---|
| Mean | 139.75 | 55.60 | 18.25 | 6.40 | 4.50 | 1.00 |

Table 3 (cont.)

| Source | df | SS | F | *p* |
|---|---|---|---|---|
| **Surface Deposit Feeders** | | | | |
| Container | 1 | 0.674 | 1.844 | 0.189 |
| Treatment | 2 | 5.367 | 7.344 | 0.004*** |
| Container x Treatment | 2 | 6.173 | 8.447 | 0.002*** |
| Error | 21 | 7.673 | | |

| Treatment | *Thalassiosira* Trays | Control Depressions | *Sargassum* Depressions | *Thalassiosira* Depressions | *Sargassum* Trays | Control Trays |
|---|---|---|---|---|---|---|
| Mean | 29.75 | 8.50 | 8.50 | 7.80 | 5.60 | 2.00 |

| Source | df | SS | F | *p* |
|---|---|---|---|---|
| **Subsurface Deposit Feeders** | | | | |
| Container | 1 | 26.378 | 46.912 | 0.000*** |
| Treatment | 2 | 53.826 | 47.863 | 0.000*** |
| Container x Treatment | 2 | 30.438 | 27.066 | 0.000*** |
| Error | 21 | 11.808 | | |

Table 3 (cont.)

| Treatment | *Thalassiosira* Trays | *Sargassum* Trays | *Sargassum* Depressions | *Thalassiosira* Depressions | Control Depressions | Control Trays |
|---|---|---|---|---|---|---|
| Mean | | | | | | |

| Source | df | SS | F | *p* |
|---|---|---|---|---|
| ***Capitella* spp.** | | | | |
| Container | 1 | 51.630 | 83.186 | 0.000*** |
| Treatment | 1 | 3.037 | 4.893 | 0.044* |
| Container x Treatment | 1 | 15.205 | 24.498 | 0.000*** |
| Error | 14 | 8.689 | | |

| Treatment | *Thalassiosira* Trays | *Sargassum* Trays | *Sargassum* Depressions | *Thalassiosira* Trays |
|---|---|---|---|---|
| Mean | 229.0 | 79.8 | 37.75 | 0.200 |

Table 3 (cont.)

| Source | df | SS | F | *p* |
|---|---|---|---|---|
| ***Nereimyra* sp.** | | | | |
| Container | 1 | 43.913 | 78.894 | 0.000*** |
| Treatment | 1 | 1.138 | 2.047 | 0.174 |
| Container x Treatment | 1 | 8.452 | 15.201 | 0.002** |
| Error | 14 | 7.784 | | |

| Treatment | *Thalassiosira* Trays | *Sargassum* Trays | *Sargassum* Depressions | *Thalassiosira* Trays |
|---|---|---|---|---|
| Mean | 127.2 | 48.2 | 12.5 | 0.2 |

*$p \leq 0.05$, **$p \leq 0.01$, ***$p \leq 0.001$

[a]All data were log (x+1) transformed to homogenize variances.

[b]Control Treatments were dropped for analysis of individual taxa because the rarity of individuals made it impossible to homogenize variances between treatments.

abundant burrowing polychaete taxa (*Capitella* spp. and *Nereimyra* sp.) were actually most numerous in enriched trays.

One explanation for generally lower numbers of organisms in depression treatments is that different trophic groups may have colonized trays and artificial depressions. Higher densities of surface deposit feeders and subsurface deposit feeders in trays coupled with higher densities of omnivores (i.e., potential carnivores) in depressions would suggest that omnivores might be reducing densities of colonizers in depressions. Results from ANOVA comparisons do not support this hypothesis. Although subsurface deposit feeders were significantly more abundant in *Thalassiosira* Trays than *Thalassiosira* Depressions, a similar effect was not observed for *Sargassum* or Unenriched Control Tray/Depression comparisons. For surface deposit feeders, densities in Unenriched Control Depressions were significantly *higher* than Unenriched Control Trays, and other Tray/Depression contrasts with similar treatments were not significantly different. Omnivores were significantly more abundant in *Thalassiosira* Trays than in *Thalassiosira* depressions, and neither of the Unenriched Control Tray/Depression and *Sargassum* Tray/Depression contrasts were significantly different.

## 4. Discussion

Highly diverse habitats, such as coral reefs and rainforests, generally tend to be spatially complex (e.g. Connell, 1978), and the deep-sea appears anomalous in its apparent homogeneity. A key factor contributing to the immense diversity of the deep

sea may be microhabitats created by small-scale patches (Grassle and Sanders, 1973). The fall of detritus in the deep sea is a variable process in time (e.g. Billett *et al.*, 1983; Lampitt, 1985) and space (Thiel *et al.*, 1990). Seasonality in detrital flux has been documented for productive regions (Billett *et al.*, 1983; Lampitt, 1985), tropical regions (Honjo, 1982) and sub-tropical oligotrophic regions (Deuser and Ross, 1980). Phytodetritus may serve as an important food source for benthic organisms (e.g. Gooday, 1988) and organisms associated with detritus, such as bacteria, cyanobacteria (Lochte and Turley, 1988), flagellates (Turley and Carstens, 1991) and ciliates (Silver *et al.*, 1978) are all potential food sources that could attract deep-sea macrofauna. A variety of other potential food sources exist, including whale (Smith *et al.*, 1989) and fish (Stockton and DeLaca, 1982; Smith, 1986) carcasses, macroalgae (Grassle and Morse-Porteous, 1987), and seagrass (Suchanek *et al.*, 1985). Without doubt, further research in the deep sea will reveal other potential carbon sources, and thus increase the possible "patch" types available to deep-sea organisms.

In an earlier paper, we presented colonization tray data in support of the patch mosaic model. Results suggested that a specialized subset of the Ambient Flat fauna responded to the colonization trays, and different faunal groups colonized different tray treatments. Many of the dominant colonizers were opportunistic, and similar responses have been observed in other deep-sea habitats (e.g. Grassle and Morse-Porteous, 1987; Grassle *et al.*, 1988). Our study offers the first evidence that different faunas colonize different patch types, which is important if a patch mosaic is indeed the reason for such high deep-sea diversity.

Depression experiments offer additional support for the patch mosaic model. *Sargassum* Depressions were clearly very different from *Thalassiosira* and Unenriched Depressions both in abundance of dominant colonizers (Fig. 4) and in faunal similarity (Figs. 5, 6). Moreover, of the depression treatments, only *Sargassum* Depressions had markedly lower diversity. *Thalassiosira* Depression fauna did not show strong differences from Unenriched Control Depressions, although it was somewhat different from Flat Ambient. Thus, different types of disturbance produced different faunal responses.

Compared with *Thalassiosira* and *Sargassum* Trays, total numbers of individuals recovered in depressions were surprisingly low (Fig. 3). Total numbers in *Thalassiosira* Depressions were even lower than in *Sargassum* Depressions, exactly the opposite result observed in trays. A similar trend is evident in comparing dominant taxa (Fig 5). With the exception of *Nebalia* sp., dominant opportunists were much more abundant in trays than depressions for a given treatment. Only Unenriched Control Depressions had higher densities of individuals compared with the corresponding tray treatment, and this was not reflected in the most abundant opportunists. Because numbers in depressions were low relative to trays, and densities differed substantially between depression treatment types, passive trapping does not appear to be an issue, at least for dominant colonizers. Thus, colonization by dominant colonizers, at least, was highly active and selective.

The absence of strong faunal differences between *Thalassiosira* Depressions and Unenriched Control Depressions, and also the low densities of individuals in

*Thalassiosira* Depressions is somewhat surprising, given the extremely high densities of opportunistic organisms observed in *Thalassiosira* Trays. One explanation for this result is that *Thalassiosira* sp. was more readily available to consumers in depressions compared to trays because it was dropped on the sediment surface rather than integrated through the top 2 centimeters. Thus, increased availability and lower amounts added (because some *Thalassiosira* sp. paste was lost during addition) may have resulted in rapid depletion of *Thalassiosira* sp. by opportunists that emigrated out of depressions before we resampled 24 days later. This could have resulted in similar faunas in Unenriched Control Depressions and *Thalassiosira* Depressions. The same sort of effect may not have occurred with *Sargassum* because particles of algae were larger (and thus less easily ingested) and this type of algae is resistant to decomposition (Sieburth and Conover, 1965).

Perhaps the most interesting result of the depression experiment was the variability of the fauna in Natural Depressions, and the clear separation of Natural Depressions from Flat Ambient fauna (Fig. 6). It is not surprising that the Natural Depressions do not form a tight, discrete grouping given that their age and history are completely unknown. What is most striking about Natural Depressions is that they have similar diversity (Fig. 7), but different species composition (Fig. 6) compared to Flat Ambient fauna. The highly diverse and different fauna present in Natural Depressions compared with Flat Ambient areas may be a result of organisms responding to differences in grain size, carbon content or many other sediment characters. Based on our artificial depression experiments, organic content could certainly be an important

difference between Natural Depressions and Flat Ambient sediment, but these other factors could also be important.

Another explanation for the generally lower densities of organisms in depressions is that predators may have been more abundant in depressions than trays, resulting in higher predation on, or active avoidance of trays by, dominant colonizers. Evidence in support of this explanation would be higher densities of predators in depressions than in trays and lower densities of surface and subsurface deposit feeders in depressions. Densities of potential predators (i.e., omnivores), however, were significantly lower in depression treatments (*Thalassiosira* and *Sargassum*) than in the corresponding tray treatments and predator densities did not differ significantly in Unenriched Control treatments. Moreover, subsurface deposit feeders were less abundant in depressions than trays in *Thalassiosira* treatments, but densities did not differ between trays and depressions for the *Sargassum* and Unenriched Control treatments. Surface deposit feeders also did not support the hypothesis of higher predation in depressions because densities were higher in *depression* treatments than in tray treatments (*Sargassum,* Unenriched Controls) and differences were not significant in the *Thalassiosira* treatments. Clearly, these results do not indicate that predators caused a reduction of densities of colonizers in depressions. This does not eliminate the possibility that large, mobile predators (e.g., fish, crabs) may have avoided trays moreso than depressions, however, to attribute all of the observed patterns to predation alone would require an extremely convoluted explanation.

Organisms could not migrate through the sediment into trays. Given that

within-sediment migration may be an important colonization mode over small scales (Smith *et al.*, 1986; Kukert and Smith, 1992), this potential bias could not be ignored. Densities of burrowers were significantly lower in Unenriched Control Trays than in Unenriched Control Depressions, and a similar difference was observed with *Sargassum* treatments (Table 2). Densities of nonburrowers did not show the same sort of trend, and nonburrowers were actually more abundant in tray treatments. These results suggest that trays do reduce colonization by burrowers, although some of the opportunistic forms (e.g., *Capitella* spp. and *Nereimyra* sp.) appear to have been able to overcome this obstacle. Opportunists were extremely abundant in trays, yet less abundant in depression treatments and relatively rare in the ambient sediment. Clearly, despite the fact that many of the dominant opportunists were potential burrowers, within-sediment migration was not the dominant dispersal mode for these taxa.

The deep sea is generally considered to be food limited (e.g., Rowe and Gardner, 1979), and the rapid response to added food resource (enriched trays and depressions) compared with the slow response to added space resource (Unenriched Trays, Unenriched Depressions) certainly suggests that food is far more limiting than space. It has been suggested that a competitive bottleneck may exist in the deep sea (Jumars *et al.*, 1990), where juveniles must compete for limited food resources to "squeeze through" the bottleneck. Mature individuals do not show much specialization in the deep sea (Dayton and Hessler, 1972), and this seems inconsistent with a high-diversity habitat. If, however, such a bottleneck exists, specialization and "weeding out" may occur at the larval and juvenile stages. Densities of competing adults may be

sufficiently low (because of the "weeding out" at the bottleneck) such that colonizing larvae are not outcompeted. The vast preponderance of juveniles in our experiments is consistent with the concept of a larval bottleneck. Although the fauna in "patches" consisted almost exclusively of juveniles, ambient fauna was largely adult, suggesting that colonization of patches was by dispersing larvae.

With a single exception (Desbruyeres *et al.*, 1980), macrofaunal colonization in the deep sea is thought to be a relatively slow process (e.g. Grassle, 1977; Levin and Smith, 1984; Desbruyeres *et al.*, 1985; Grassle and Morse-Porteous, 1987) relative to shallow-water systems. However, these studies have been conducted over time scales of many months, and in some cases have not used any form of enrichment. It is possible that carbon pulses may produce rapid responses followed by emigration, and these dynamics may be missed over longer time scales. Studies of deep-sea species response over varying periods of time are sorely lacking, and would undoubtedly produce interesting data. The rapid macrofaunal response observed in our colonization trays over a very short time period (23 days) suggests that important community dynamics may occur over very short time scales, particularly where organic pulses are involved. *Thalassiosira* Depressions and Unenriched Control Depressions showed only weak differences from Flat Ambient fauna, suggesting that the recovery after small disturbances and "patch" formation may be rapid. Evidence from other work also suggests that some events in the deep sea may occur more quickly than was once thought. Megafaunal organisms respond to carcass falls within hours (e.g., Smith, 1986), perhaps explaining why carcasses are observed so rarely from submersibles

(Grassle and Morse-Porteous, 1987). Macrofauna respond to artificial mounds within months (Smith *et al.*, 1986), and Foraminifera may respond to seasonal phytodetritus over a similar time period Gooday, 1988). Infaunal benthos can incorporate significant amounts of organic carbon in days (Graf, 1989).

There are two other explanations for our high colonization densities compared to previous deep-sea studies; the sieve size used in this study was very small and trays were placed flush with the sea floor. The use of a small sieve size (63 μm), cannot explain the difference in results because most individuals (>95%) were retained on a 300-μm screen that is comparable to sizes used in other studies. Near-bed hydrodynamics may influence settling larvae (e.g. C.A. Butman, 1987), and the disruption of boundary-layer flow by protruding trays may have reduced numbers of settling larvae in previous deep-sea studies. However, if colonizers are sensitive to near-bed flow strictly as a result of passive transport, then substantially higher colonization would be expected in depressions compared with trays. It is possible that larvae may actively avoid elevated trays or simply never encounter them, particularly if larvae swim close to the bottom.

Although higher densities of organisms were not observed in depression treatments compared with tray treatments, it is still possible that near-bed hydrodynamics may influence deep-sea colonization processes. For most species, too few individuals were present to draw any conclusion concerning passive trapping. Even for abundant species, however, it is unclear whether near-bed hydrodynamics may modify settlement patterns. In a flume study of two shallow-water species, larval

settlement was selective, but probability of encounter with the sediment was enhanced in depressions (Snelgrove *et al.*, in press). Thus, hydrodynamics were important in transporting larvae to the sediment, at which point larvae exhibited selectivity. It is possible that transport of larvae to depressions in our deep-sea experiments may also have been enhanced, but larvae were able to escape if the organic matter was either unsuitable (early stage of the experiment) or perhaps after organic matter had become relatively depleted (later stages of the experiment). Clearly, however, dominant taxa could escape if they so desired.

A critical difference between shallow- and deep-water systems is the persistence of patches. In shallow-water systems, patches may last from hours to weeks before rapid biological reworking of sediment (e.g., Rhoads, 1963) or physical processes (e.g., B. Butman, 1987) obliterate the patch. At the St Croix site, depressions created by box coring in 1989 were visible and similar to their original shape when we returned to the site in October 1991. Thus, the transient nature of such patches in shallow water may limit faunal specialization on patches, particularly for populations with short reproductive periods. The long-term persistence of patches in the deep sea allows opportunity for specialization and succession, perhaps more specifically for juveniles than adults. Detailed examination of different patch types over time and response of juveniles may be the key to understanding deep-sea biodiversity.

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# CHAPTER 7

## The Contribution of Temporal Changes in Disturbance Patches to the Maintenance of High Deep-Sea Diversity: Colonization Tray Experiments

*Abstract* - To determine whether age of small-scale food patches affects colonization of deep-sea macrofaunal communities, we deployed colonization trays by submersible at 900 m depth for 23 d and 29 mo. Treatments were prefrozen, natural sediment that was unenriched or enriched with *Sargassum* sp. Short-term *Sargassum* treatments contained significantly higher total densities of organisms than the ambient sediment, and short-term unenriched treatments had significantly lower densities than the ambient sediment. In long-term experiments, total densities in both treatments were higher than in ambient sediments and densities in unenriched trays were higher than in *Sargassum* treatments, but differences were not significant. Total densities were higher in long-term unenriched treatments than in short-term unenriched treatments, and although mean densities in short-term *Sargassum* treatments were higher than in long-term treatments, variances were very high. Ambient faunal densities did not change between the short- and long-term experiments. Multivariate analyses indicated that short- and long-term *Sargassum* treatments both attracted high densities of a relatively low-diversity fauna, but the faunas differed markedly in species composition. Short-term, unenriched treatments attracted low densities of a high-diversity fauna and long-term unenriched treatments attracted high densities of a moderately diverse fauna which resembled that observed in long-term *Sargassum* treatments. All of the treatments showed low faunal affinity with the ambient community. Results indicate that different faunas may colonize patches of different ages, suggesting that, in addition to differences in patch type, age of patches may be an important source of microheterogeneity in the deep-sea. By specializing on different patches, large numbers of species may be able to coexist. This may be an

important difference between low diversity shallow-water ecosystems and deep-sea communities.

Deep-sea macrofaunal communities are extremely species rich (Grassle and Maciolek 1992). Compared with other species-rich habitats such as coral reefs and tropical rain forests, however, the deep sea appears to lack the obvious spatial and temporal complexity that contribute to diversity in these other habitats. One explanation for this paradox is that small-scale patches of food and disturbance create microhabitats in space and time, allowing specialized species response and coexistence of large numbers of species (Grassle and Sanders 1973). Evidence for patchiness in deep-sea ecosystems is rapidly accumulating (e.g. Billett et al. 1983; Suchanek et al. 1985; Smith et al. 1986; Grassle and Morse-Porteous 1987), and the combined effects of limited food resources and persistence of patches over time in the deep sea may magnify the importance of patchiness relative to shallow-water ecosystems (e.g., Grassle and Morse-Porteous 1987).

In a previous paper, we presented results from colonization tray experiments conducted at 900 m depth near St. Croix, U.S. Virgin Islands that showed different macrofaunal response to different patch types (Snelgrove et al. 1992). Trays that were filled with prefrozen sediment and either unenriched or enriched with *Sargassum* sp. or *Thalassiosira* sp. were colonized by markedly different faunas over 23 d., and the species that were abundant in trays were rare in the ambient sediment. These results clearly suggest that different species respond to different patch types, and that this may be an important aspect of deep-sea diversity.

Although there are many different types of organic input that could contribute to a patch mosaic in the deep sea, another potentially important aspect of patchiness

may be temporal dynamics as patches age. Older patches may support very different faunas than newly created patches for a variety of reasons, including changes in amount and composition of organic matter in the patch, succession of colonizing species, or chance encounters over time by different colonizers that occur in low abundances. The goal of the present study was to evaluate changes in faunal composition in artificial "patches" over time. Colonization trays were left on the sea floor for a short term (< 1 month) and a long-term (> 2 years) experiment.

Colonization experiments were conducted at 900 m depth in an area 14.4 km southwest of St. Croix (17°35.38'N, 64°47.52'W). Trays consisted of a central cup (10-cm deep, 11.3-cm diameter) surrounded by a Delrin collar (40-cm diam). The central cup was filled with sediment, resulting in a sediment surface area of 100 $cm^2$. A sealing lid was attached to the trays during deployment and recovery, allowing quantitative recovery of colonizing fauna. Trays were designed to be placed flush with the ocean bottom to reduce potential hydrodynamic bias associated with trays that protrude above the bottom into the boundary layer. A more detailed description of the tray design and flume simulations of flow over trays, is given in Snelgrove et al. (1992).

For long- and short-term experiments, trays were filled with prefrozen sediment collected from the site that was either unenriched (Unenriched Control treatments) or enriched with *Sargassum* sp. (*Sargassum* treatments). *Sargassum* sp. was chosen as an enrichment because it is known to accumulate on the deep-sea floor in several habitats (Suchanek et al. 1985; Grassle and Morse-Porteous 1987). The *Sargassum* that was used in these experiments was collected from surface waters off the coast of Florida and

frozen. Before the *Sargassum* was mixed through the top 2 centimeters of sediment in trays, it was ground into a mulch to avoid the hydrodynamic complication of algae protruding above the sediment surface. Unenriched Control treatments mimicked defaunation disturbance without organic input, such as fish feeding. In total, 5 replicates each of short-term *Sargassum* and Unenriched Control treatments and 3 replicates each of long-term *Sargassum* and Unenriched Control treatments were successfully deployed and recovered. Short-term treatments (23 days) were deployed in May and recovered in June of 1989; long-term treatments (29 months) were deployed within a few days of recovering the short-term treatments and were recovered in 1991. Three trays were deployed on a single dive, and treatments were interspersed haphazardly along a transect to eliminate any treatment-specific time and location effect. Trays were placed at distances of 2-3 m to >10 m apart along a transect that ran perpendicular to the station marker. Long-term treatments were deployed in the vicinity of short-term treatments the day after the short-term treatments were recovered. Thus, comparisons between short- and long-term experiments are based on the assumption that the lack of overlap in deployment times between experiments did not contribute to faunal differences. The fauna in the ambient sediment was sampled in 1989 (5 replicates) and 1991 (3 replicates) using an ALVIN-style box corer (e.g. Grassle and Morse-Porteous 1987), that encloses an area of 225 $cm^2$ and penetrates to $\approx$ 10 cm . The upper 2 cm of trays and box cores were sieved aboard ship over a 63-µm sieve and then preserved in buffered 4% formaldehyde. Samples were later transferred to 80% ethanol, stained with Rose Bengal, and sorted under a dissecting microscope. Organisms were identified to the

lowest possible taxonomic level, which was often limited by the absence of mature specimens. Meiofaunal taxa and protozoans were not enumerated.

Total faunal abundances, abundances of dominant species, faunal similarities, and diversity were compared between treatments. Within the short- and long-term experiments, total densities in treatments and ambient sediment were compared with the ANOVA model $y = \mu + \text{Treatment} + \text{Error}$, where $\mu$ is the constant and Treatment refers to *Sargassum* treatments, Unenriched Control treatments or ambient sediment. A Tukey's HSD Multiple Comparisons test was used to determine which means differed. For individual taxa, even the most abundant species had zero variance (no individuals in any replicates) in some treatments, making statistical comparison problematic. Therefore, mean densities and standard errors are presented for the 4 most abundant taxa. Faunal similarity between samples was compared using group-average clustering and nonmetric multidimensional scaling of NESS (Normalized Expected Species Shared) similarities (Grassle and Smith 1976). Diversity was calculated using Hurlbert rarefaction because it is the least problematic of the diversity measures and is sensitive to rare species that are such an important component of deep-sea assemblages (e.g. Grassle and Morse-Porteous 1987).

Total densities of macrofauna were markedly different between treatments and experimental durations (Fig. 1). In short-term experiments, *Sargassum* treatments had significantly higher densities than the ambient sediment, and Unenriched Control treatments had significantly lower densities than the ambient sediment (Table 1). Within long-term experiments, *Sargassum* treatment mean densities were higher than in

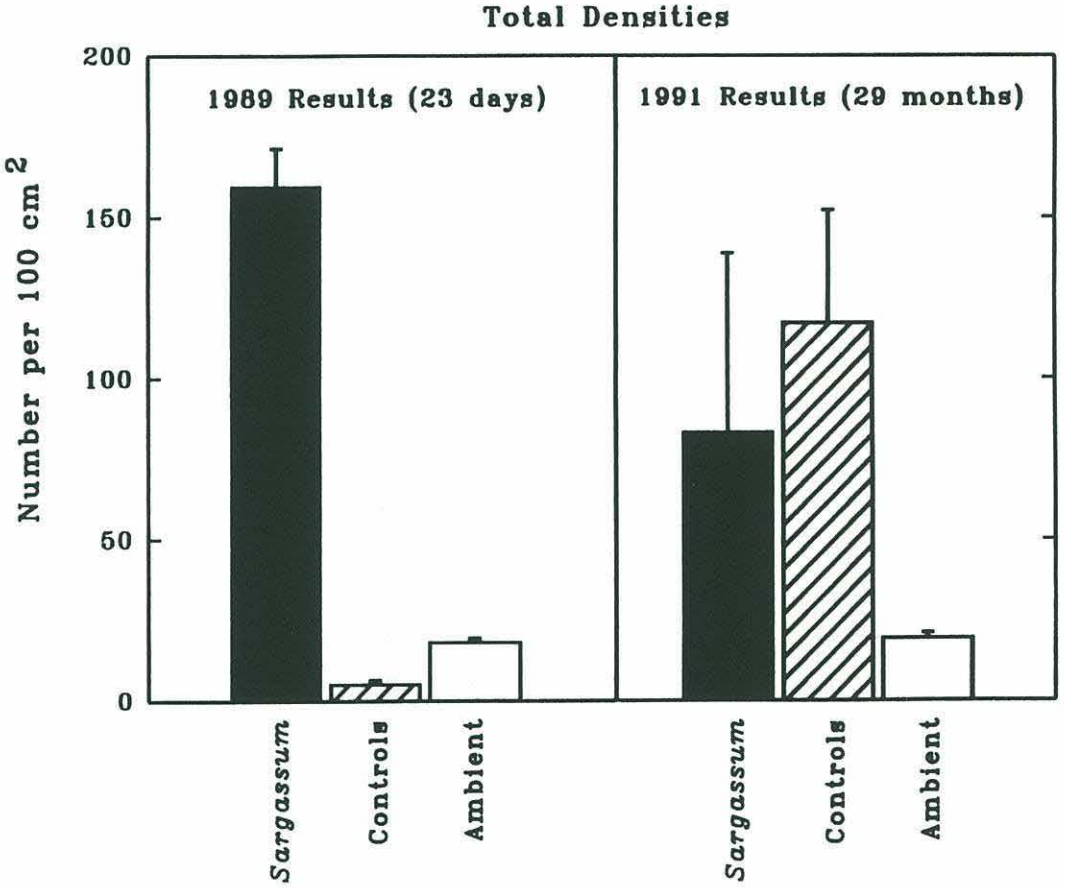


Figure 1. Bar graph showing total densities and one standard error for taxa colonizing *Sargassum* Trays (n = 5) and Control Trays (n = 5) over 23 days in 1989 and *Sargassum* Trays (n = 3) and Control Trays (n = 3) over 29 months ending in 1991 relative to ambient fauna during the 23 day experiment in 1989 (n = 5) and at the end of the 29 month experiment in 1991.

TABLE I

ANOVA results for total densities in ambient sediment compared between 1989 and 1991, and ANOVA results for total densities of organisms compared separately among short-term treatments (*Sargassum*, Controls, and Ambient fauna) and long-term treatments and results of Tukey-Kramer tests for significant treatment effects. Densities were log (x+1) transformed to homogenize variances.

| Source | df | SS | F | p |
|---|---|---|---|---|
| **Total Ambient Densities** | | | | |
| Year | 1 | 0.009 | 0.363 | 0.569 |
| Error | 6 | 0.144 | | |
| **Short-term Experiment** | | | | |
| Treatment | 2 | 29.462 | 129.061 | 0.000*** |
| Error | 12 | 1.370 | | |
| **Long-term Experiment** | | | | |
| Treatment | 2 | 4.316 | 4.098 | 0.075 |
| Error | 6 | 3.159 | | |

*$p \leq 0.05$, **$p \leq 0.01$, ***$p \leq 0.001$

| Tukey-Kramer test | **Short-term Experiment** | | |
|---|---|---|---|
| Treatment | *Sargassum* | Ambient | Controls |
| Mean | 159.8 | 18.0 | 5.0 |

Unenriched Control treatments which were higher than the ambient sediment, but none of the differences was significant. Unenriched Control treatments showed a marked increase in faunal densities between the short-term deployments, where densities were extremely low, and the long-term deployments, where densities were actually higher than those in long-term *Sargassum* treatments. During the short- and long-term experiments, ambient faunal densities did not change (Table 1).

The most abundant species in trays were generally rare in the ambient environment (Fig. 2), and the dynamics of the dominant taxa were somewhat different among treatments. The polychaetes *Capitella* spp. and *Nereimyra* sp. and the crustacean *Cumella* sp. showed similar patterns in short-term experiments; high numbers were observed in *Sargassum* treatments, but very low numbers were observed in Unenriched Control treatments and the ambient sediment. *Aricidea* sp., however, was not found in short-term *Sargassum* or Unenriched Control treatments but was modestly abundant in the ambient sediment. In long-term treatments, *Aricidea* sp. was abundant in *Sargassum* and Unenriched Control treatments, and densities of *Cumella* sp. and *Nereimyra* sp. were very low. *Aricidea* sp. was also the only abundant taxon in trays that was somewhat common in ambient samples. *Capitella* sp. was fairly common in long-term Unenriched Control treatments, unlike in short-term Unenriched Control treatments where it was virtually absent, however, densities in long-term *Sargassum* treatments were somewhat lower than in short-term *Sargassum* treatments. Thus, there appeared to be a shift in dominant species within each treatment over time. The short-term *Sargassum* and Unenriched Control treatments had markedly different abundances of dominant taxa,

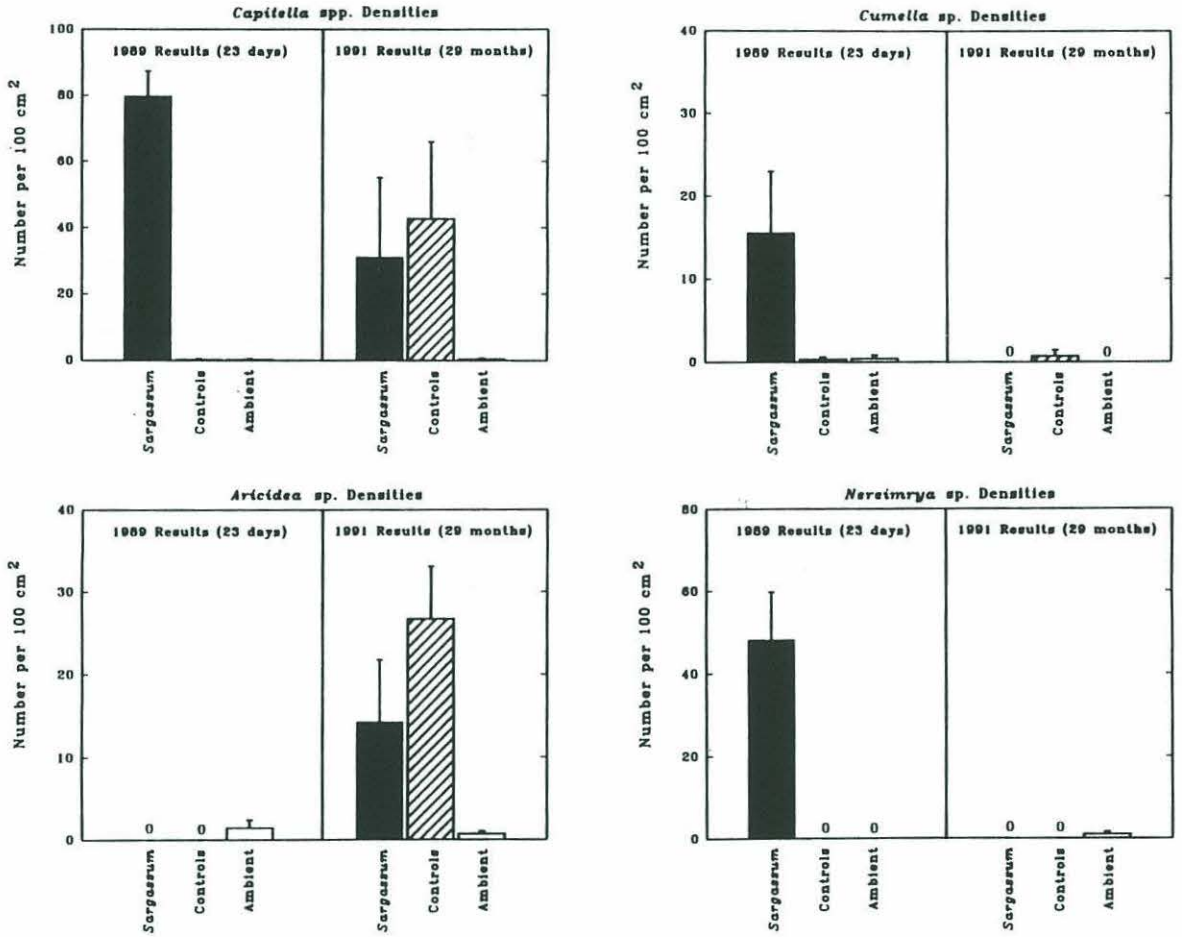


Figure 2. Bar graph showing mean densities and one standard error for the most common species colonizing 23 day and 29 month deployments of *Sargassum* Trays and Control Trays relative to ambient densities at the time the experiments were terminated. Sample sizes are given in caption for Figure 1.

however, as abundances in Unenriched Control treatments increased over time and abundances in *Sargassum* treatments decreased, the two treatments became more similar.

Group-average clustering of NESS similarities indicated two major clusters; one cluster contained all of the ambient samples, and the other cluster contained all of the tray experiments (Fig. 3). Within the tray cluster, short-term *Sargassum* treatments were clearly different from long-term *Sargassum* and Unenriched Control treatments. Short-term Unenriched Control treatments were not included in the analysis because so few individuals were collected, however, based on their extremely low densities, short-term Unenriched Control treatments were markedly different from any of the other treatments. Long-term *Sargassum* and Unenriched Control treatments showed poor separation, suggesting that the long-term treatments had similar faunas after 2.4 years. Results from the multidimensional scaling analysis supports results obtained from the clustering analysis (Fig. 4). Faunas in short-term *Sargassum* treatments and the ambient fauna each formed separate clusters, and long-term *Sargassum* and Unenriched Control treatments were very similar.

Rarefaction curves indicated different patterns of diversity within the short-term and long-term experiments (Fig. 5). Short-term Unenriched Control treatments had a fairly high faunal diversity comparable to the high-diversity ambient environment, however, short-term *Sargassum* treatments had very reduced diversity. Diversity of long-term Unenriched Control treatments was lower than long-term *Sargassum* treatments, but diversity in both long-term treatments was substantially lower than the ambient fauna. Thus, short-term Unenriched Control treatments were characterized by

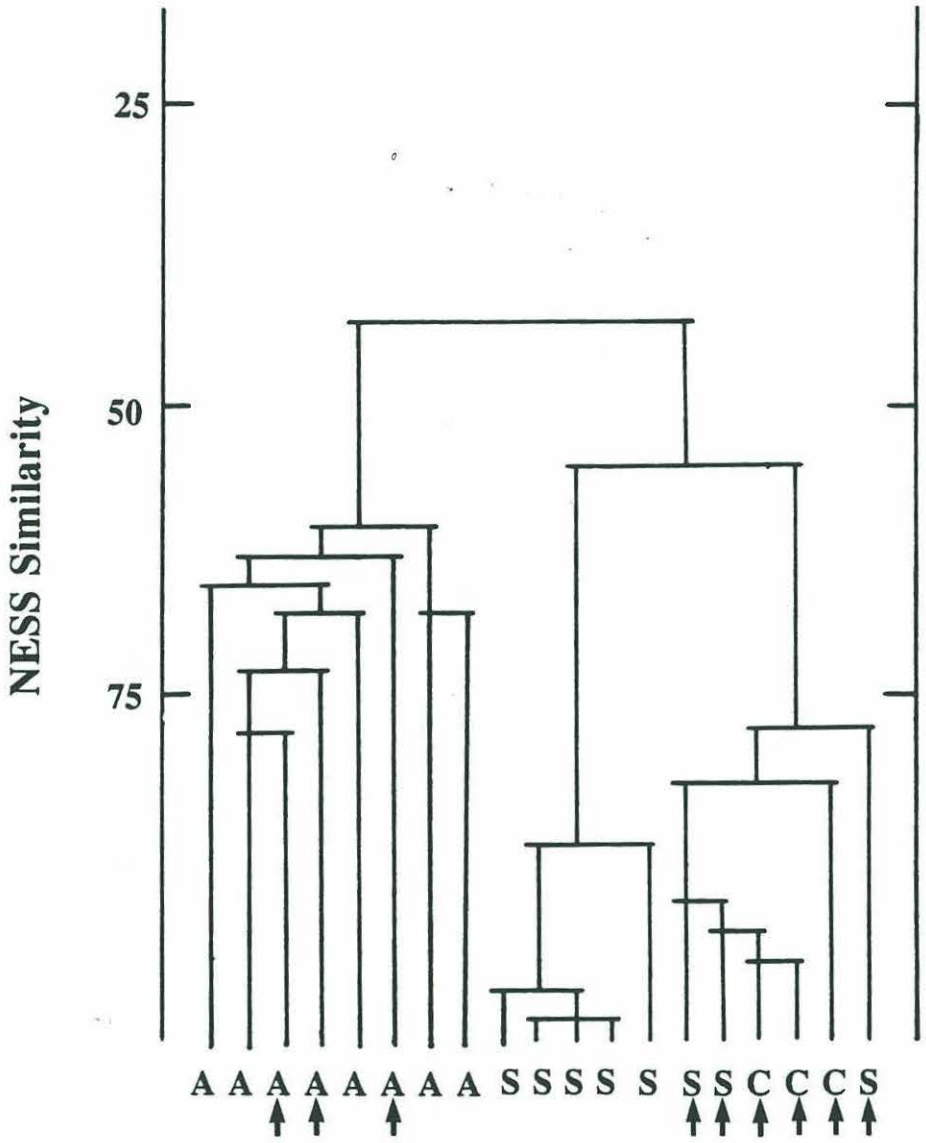


Figure 3. COMPAH group-average clustering of NESS (Normalized Expected Species Shared) similarities of short- and long-term tray deployments and ambient fauna based on a random draw of 10 individuals. A = ambient fauna, S = *Sargassum* Trays and C = Control Trays. Arrows indicate 29 month trays and 1991 ambient samples. Control Trays from 1989 (23 day deployments) were not included in the analysis because too few individuals colonized trays.

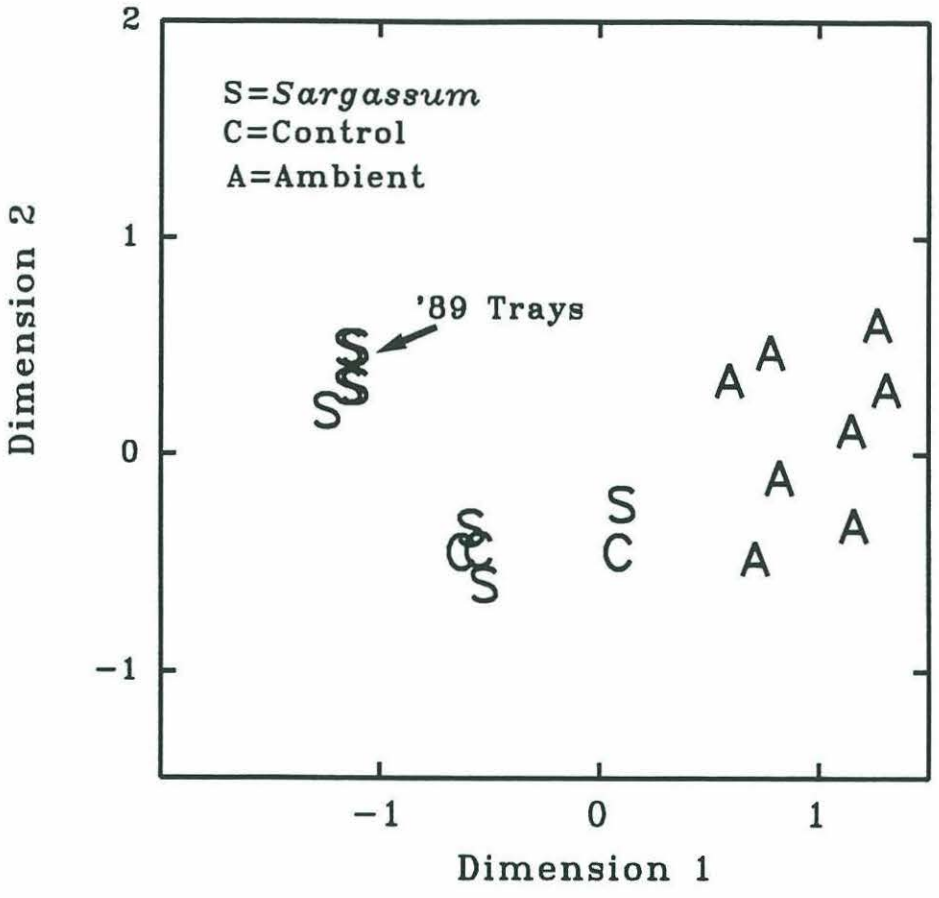


Figure 4 Nonmetric multidimensional scaling in two dimensions of short- and long-term tray deployments and ambient fauna based on NESS (Normalized Expected Species Shared) similarities generated from a random draw of 10 individuals. Stress value of the plot is 0.088. A = ambient fauna, S = *Sargassum* Trays and C = Control Trays. Arrow with "'89" indicates 23 day *Sargassum* Trays. Control Trays from 1989 could not be included in the analysis because too few individuals colonized trays. Ambient samples from 1989 and 1991 are not differentiated because they showed no differences from one another.

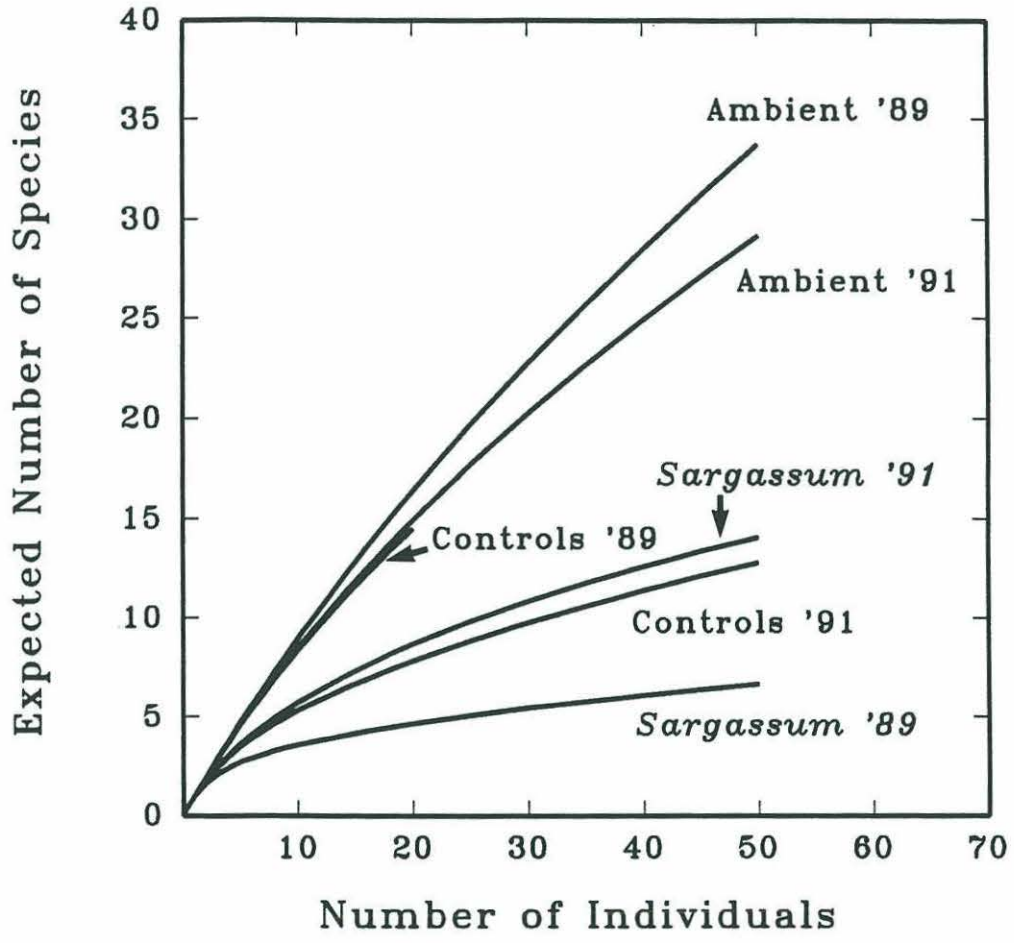


Figure 5. Number of Individuals plotted against Expected Species (Hurlbert rarefaction) for each tray treatment and ambient fauna. Each curve is based on random combinations of replicates of each treatment. "'89" refers to 23-day tray deployments in 1989 or ambient samples collected in 1989 and "'91" refers to 29 month deployments recovered in 1991 or ambient samples collected in 1991.

low densities of a high-diversity fauna, however, over time this fauna became less diverse as densities increased and more opportunistic species arrived. Short-term *Sargassum* treatments were characterized by high densities of a low diversity fauna which became more diverse as densities decreased slightly over time. Thus, the faunas in the two treatments became more similar over time.

The trends observed in different treatments in each experiment and the convergence of faunas in long-term *Sargassum* and Unenriched Control treatments suggests that the dynamics associated with colonization of patches may be very complex. Densities of colonizers increased in Unenriched Control treatments between 23 day and 29 month deployments, and densities in *Sargassum* treatments decreased over the same time period. These results are difficult to interpret in terms of temporal change, and suggest that colonization experiments that look at only one time interval may provide an even more ambiguous view of colonization processes. Neither treatment resembled background fauna after 23 days or 29 months, although one common ambient species (*Aricidea* sp.) was abundant in long-term but not short-term treatments. Thus, over time trays may have started to lose strictly opportunistic organisms and gain fauna that was more consistent with background communities. It is not surprising that in *Sargassum* treatments, densities were lower in long-term relative to short-term deployments because *Sargassum* probably became depleted over time. The high densities of opportunistic (e.g. *Capitella* spp.) and non-opportunistic (e.g. *Aricidea* sp.) fauna in Unenriched Control treatments in long-term experiments compared to short-term experiments suggests that in addition to organic matter, space may also be an

important resource to some species in deep-sea systems. It is also possible, however, that organisms may have responded over the long term to very modest levels of enrichment in Unenriched Control treatments resulting from organisms that were killed in the sediment when it was frozen. The decrease in densities of opportunists and abundance of juveniles in long-term *Sargassum* treatments suggests that the initial juveniles that colonize over short time periods (e.g., 23 days) may either die or emigrate out of trays over longer time periods (e.g., 29 months), perhaps because of predation or competitive pressures. The absence of potential competitors might also explain why long-term Unenriched Control treatments attracted high densities of opportunists relative to the ambient community; despite the lack of a rich carbon source, opportunists did eventually colonize Unenriched Control treatments where adults of other taxa were absent.

These experiments expand on previous research suggesting that different fauna respond to different types of "patch" (Snelgrove et al. 1992), and indicate that the fauna within a given patch type may change considerably over time. Reasons why faunal composition may change include changes in the quality of organic matter, colonization by bacteria, and/or macrofaunal succession, but these experiments offer no way of distinguishing between the relative importance of these processes. Results do indicate, however, that aging of patches may affect deep-sea diversity by providing microhabitats in addition to those created by different patch types. Evidence for existence of qualitatively different patch types in deep-sea ecosystems is increasing, and patches may be created by seasonal detrital flux (Billet et al. 1983) to transport of seagrasses (e.g.

Suchanek et al. 1985) and algae (Grassle and Morse-Porteous 1987) from surface waters, to physical disturbances such as feeding mounds (e.g. Smith et al. 1986).

The long-term experiments support previous findings of unusually rapid colonization at this site (Snelgrove et al. 1992). The long-term experiments were colonized by substantially higher densities of organisms than have been observed in long-term colonization tray experiments conducted in other areas of the deep sea (e.g. Grassle 1977; Desbruyères et al. 1985; Grassle and Morse Porteous, 1987), even in the absence of organic enrichment. Colonization rates in our short-term experiment was faster than other short-term, deep-sea deployments (Grassle, 1977; Levin and Smith 1984; Desbruyères et al., 1985; Grassle and Morse-Porteous 1987). Differences in geographic may explain these high colonization rates. Furthermore, out study site was substantially shallower than these other areas. Densities of ambient fauna are roughly comparable between studies, however. Other differences between this study and others are the fine screen size (63 µm) used in sieving our samples, and the placement of trays flush with the bottom rather than elevated into the boundary layer. It is unlikely that screen size explains density differences because we found that most individuals were retained on a 300-µm screen when nested sieves were used (see Snelgrove et al. 1992). The placement of trays flush with the bottom may be important, however, given that near-bed hydrodynamics are thought to have important effects on settling larvae in shallow-water habitats (e.g. Butman 1987) and trays elevated above the bottom cause considerable flow disturbance (Snelgrove et al. in prep). Indeed, most of the individuals observed in colonization trays in our study were larvae or juveniles, and these life stages

may be particularly vulnerable to near-bottom flow disturbances.

The relatively rapid colonization rates in this study suggest that response to disturbance and organic matter in the deep sea is not necessarily slow, although rates were considerably slower than in shallow-water habitats. Nonetheless, even after 29 months, faunal composition and diversity in Unenriched Control and *Sargassum* treatments were still markedly different than that in the ambient environment, suggesting that effects of patches of organic matter and disturbance may be much more persistent in deep-sea than in shallow-water ecosystems. Even after 29 months, small pieces of *Sargassum* sp. were present in *Sargassum* treatments, and the depressions created by box coring in 1989 looked no different in 1991 when we returned to the site. The persistence of patches over such a long time period may represent a fundamental difference between deep-sea systems and shallow-water habitats, where bioturbation and storm events obliterate patches over a much faster time scale. The persistence of patches in the deep sea may allow specialization by colonizers. Thus, larval colonizers may be able to "squeeze through" a "larval bottleneck" and avoid intense competition with other species (Jumars et al. 1990; Snelgrove et al. 1992). This mechanism may explain why deep-sea communities are so diverse relative to their shallow-water counterparts.

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## General Conclusions

1. Although many studies have documented a general association between many species and the sediment in which they reside, the mechanism(s) responsible for this association is poorly understood. Clearly defined experimental studies are sorely needed to clarify cause and effect.

2. Flume experiments with the polychaete *Capitella* sp. I and the bivalve *Mulinia lateralis* indicated that flow environments designed to entrain passive particles (depressions) contained higher densities of settled larvae than flush, non-entraining environments containing a similar sediment treatment. Comparisons of settlement in a "desirable" substrate (New Bedford Harbor Mud) and an "undesirable" substrate (Glass Beads) indicated that *Capitella* sp. I larvae could "escape" from undesirable depressions, however, *M. lateralis* larvae were sometimes unable to "escape". These results suggest that hydrodynamics may modify settlement patterns and that distribution patterns for these species may be determined by the combined effects of active selection and hydrodynamic transport.

3. Field experiments at a muddy station in Buzzards Bay indicated that small-scale depressions designed to hydrodynamically trap passive particles contained higher densities of a variety of colonizing taxa than flush, non-trapping treatments. Although

these experiments did not eliminate the potentially confounding effect of organic matter accumulating in the trapping environment, an enrichment experiment indicated that active response by settling larvae was a less likely explanation than passive entrainment of larvae in depressions. Thus, it appears that near-bed hydrodynamics may influence settlement patterns for field populations of several taxa.

4. Flume simulations of flow over different types of colonization mudboxes indicate that structures that protrude above the natural ocean bottom may cause considerable flow disturbance, resulting in complex flow that bears little resemblance to natural flows. For studies in which hydrodynamic processes may play an important role (e.g., recruitment) these biases may seriously affect results, however, this potential bias can be substantially reduced with careful design consideration.

5. Colonization tray experiments at 900 m in the deep sea indicate that different fauna respond to different types of organic enrichment, and this fauna differs substantially from the natural, ambient fauna. These results suggest that small-scale patches in the deep sea may be an important source of heterogeneity, and may offer microhabitats to colonizing species and thus enhance diversity.

6. Experiments with artificial depressions and colonization trays at 900 m in the deep sea indicate that larvae did not passively accumulate in an entraining environment (depressions) and that different fauna actively colonized different treatments depending

on presence and type of organic matter. Natural depressions were also found to have unique faunas that differed from flat ambient areas, suggesting that natural forms of disturbance and patchiness may enhance deep-sea diversity.

7. Short- and long-term colonization studies at 900 m depth in the deep sea indicate that as "patches" age, different faunas are observed, suggesting that both patch type and age may be important sources of heterogeneity in the deep sea.